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History of the Larch Sawfly, with Notes on Origin and Biology^{1,2}

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The larch sawfly, *Pristiphora erichsonii* (Htg.), is currently considered a major forest insect pest in Canada. At the present time within Canada, the sawfly reacts to parasitism by *Mesoleius tenthredinis* Morley in two ways. In Manitoba and Saskatchewan the sawfly encapsulates approximately 100 per cent of the parasite eggs deposited, whereas in British Columbia encapsulation rarely exceeds four per cent (Muldrew, 1953). The reasons for the difference in degree of encapsulation are apparently unknown; however, since the origin of the sawfly itself is obscure, the possibility exists that a native species, an introduced species, or a combination of both may be present, or that geographical or ecological units may have arisen. Studies now under way by officers of the Forest Biology and Entomology divisions are attacking the problem of identity and origin following the pattern established for the European spruce sawfly, *Diprion hercyniae* (Htg.). In this instance, as with the larch sawfly, parasites were introduced on the assumption that the pest had been introduced from Europe. Critical investigations by Reeks (1941) and Balch, Reeks, and Smith (1941), involving morphological, cytological, and other biological characters, showed that the species occurring in North America was one of two species common in Europe, and previously referred to there as *Gilpinia polytoma* (Htg.). Balch *et al.* (1941) showed that *D. hercyniae* had been introduced into North America.

Taxonomic History

The following is a review of the taxonomic history of the sawfly.

Hartig (1837, pp. 187-188) gave the original description from one adult female specimen collected by Saxesen in the Harz Mountains, Germany. He placed *erichsonii* in the genus *Nematus*, set up by Jurine in 1807. Ratzeburg (1844, pp. 121-122) used Hartig's description of the species. Konow (1890), in revising the Tenthredinidae of Europe, removed some species from the genus *Nematus* and placed them in the newly established genera *Lygaeonematus* and *Holcocneme*. At this time, he placed *erichsoni* in the genus *Lygaeonematus* and used a single "i" in the trivial name. Variations in the ending of the trivial name have continued on both continents. Konow (1904) revised the genus *Lygaeonematus* and removed *erichsoni*, and later (Konow, 1904-06, pp. 61-62) included *erichsoni* in the genus *Holcocneme*. The early studies in North America paralleled the European work.

Cresson (1880) described the sawfly in North America and called it *Nematus notabilis*. In his later work (1887) on the fauna of America north of Mexico he separated *notabilis* from *erichsonii*, as referred to by Provancher (1885). Hagen (1881) described the larvae as of *N. erichsoni*. Packard (1890) redescribed the species, using Hartig's nomenclature. Later, Marlatt (1896) revised the nematines of North America and included *erichsonii* in the genus *Lygaeonematus* Konow.

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At this time Marlatt considered Hartig's *N. erichsoni* and both Cresson's *N. notabilis* and Hagen's *N. erichsoni* (from larval descriptions) as synonyms.

Studies after the turn of the century continued on both continents, with a greater interchange of information. Konow (1904-06, pp. 61-62, 66) retained *erichsoni* in the genus *Holcocneme* but placed Cresson's *notabilis* and Hagen's *erichsoni* as a single form in the genus *Lygaeonematus*, probably considering that it was North American. Enslin (1918, pp. 368-370) placed *erichsonii* in the genus *Nematus*, attributed to Panzer 1801, and considered *Nematus* and *Holcocneme* synonymous. Hewitt (1912) retained the genus *Nematus*, probably because of his affinity with some European workers. MacGillivray (1916), on the other hand, accepted Konow's genus *Lygaeonematus* for this species. In his generic classification Ross (1937), in North America, placed *erichsonii* in the genus *Pristiphora* Latreille (= *Lygaeonematus* Kon.); he wrote of the specialized Nematinae, among which he included *Pristiphora*: "This entire group of genera is in a chaotic condition taxonomically. The conventional specific differences of head sculpture and body color etc. are entirely inadequate for the task".

Dobrodeiev (1921), in Russia, and Escherich (1942, pp. 179-186), in Germany, preferred to leave *erichsonii* or *erichsoni* in the genus *Nematus*. Benson (1950), in England, followed Ross's (1937) revision, which places this species in *Pristiphora* Latreille.

Early Records and History of Infestations

In continental Europe the larch sawfly occurs from Sweden and Russia in the north to France and Switzerland in the south. It is also present in Siberia, Japan, Great Britain, the United States of America, and Canada, and thus it is truly a Holarctic species.

Europe

The sawfly was discovered in Europe in 1835, when Saxesen collected the species in the Harz Mountains of Germany. In 1838, Tischbein recorded a heavy infestation in Holstein, Germany (Escherich, 1942, p. 185). According to Thielmann (1939) the insect occurred in Holland as early as 1869; and André (1879-1882, p. 103) reported the pest from France. Records of infestation from Norway and Sweden (Thielmann, 1939) and Finland and Russia (Dobrodeiev, 1921) date from 1902 to 1915. The pest has been common but seldom destructive in the Baltic States, as observed by the junior author and as reported from Austria by Berland (1947, p. 318). In England, Cameron (1885, p. 51) stated that the earliest records dated back to the 1870's; the infestation of 1904 to 1912, however, is best known (MacDougall, 1906; Long, 1913). MacDougall (1912) also reported the sawfly from Scotland and Wales in 1912.

Asia

The first record of the sawfly in Asia was made by Polyakov (1928), who recorded it from Siberia in 1913. Severe infestation of larch near Omsk continued through 1921 and then declined. Very little information is available from Japan; however, large numbers of the cocoons were collected by the Bureau of Entomology and Plant Quarantine, United States Department of Agriculture, in the mid 1930's to obtain parasites.

North America

The first authentic record of its occurrence in the United States was made by Cresson (1880) in 1880, from Massachusetts. Annual records for the north-eastern states followed closely, in 1880 from Maine (Packard, 1883) and in 1882

and 1883 from New Hampshire and New York respectively (Packard, 1883). In 1915, the insect was first noted in Connecticut, although Britton (1916, pp. 125-134) indicated that it had undoubtedly occurred there for many years. In Michigan, the first record was made in 1906 according to Graham (1952, pp. 213-216), and in Minnesota in 1909 (Ruggles, 1911), although evidence of defoliation in previous years was observed. These late dates mark either the movement of entomologists westward or, as some scientists believe, the spread of the sawfly from east to west.

The pattern of early records in Canada (Fig. 1) follows the same general trend as in the United States. The first authentic records of occurrence of the sawfly were made by Provancher (1886) and Fyles (1884), who recorded the pest in 1882 and 1883 from Quebec City, Quebec. Details of the infestation of 1884 to 1906 are given in the writings of Provancher (1886), Fyles (1907), Jack (1887), and Fletcher (1885; 1888, p. 40; 1893, p. 147; 1906, p. 189).

The insect was first recorded from Ontario in 1884 (Fletcher, 1885); by 1900 it had been observed at both western and northern points. Hutt (1899) observed the sawfly at Bradford and Guelph in 1898, and stated that it had made considerable progress westward. Jarvis (1904) observed an infestation in the Abitibi area in 1903, and stated that the shores of Nighthawk Lake were covered with bodies of the adults. In 1908, the insect was reported from the Port Arthur-Nipigon area by Bethune (1909). Ross and Caesar (1932) reported general infestation of larch by the insect throughout southern Ontario in 1931. The sawfly began increasing in northern Ontario in 1936; large populations are still being recorded.

In New Brunswick, the earliest record was from the Dalhousie area in 1884 (Fletcher, 1885). Fletcher (1893) reported large populations in 1892 and according to Hewitt (1917a, p. 50) the insect was abundant all over the province in 1912. Very few were observed in 1929. However, an increase was noted from 1931 to 1936. The infestation began to decline in 1939 and 1940 and at present the insect is scarce. The history of infestation in Nova Scotia is similar to that in New Brunswick. According to Fletcher (1906) the insect was evidently present in Prince Edward Island during the outbreak of 1882-85 and again in 1904.

The first general record for Newfoundland was made in 1910 (Hewitt, 1911), and Brown (1939) reported severe infestations in 1939. In Labrador, Fletcher (1906), in his historical account, stated that there was an infestation of this insect from 1882 to 1885. Hewitt (1912) recorded its presence in Labrador in 1910 and Brown (1939) in 1939. A similar situation is reported by Fletcher (1906) for the Hudson Bay area.

In 1909, Hewitt (1910) recorded the pest as far west as Winnipeg in Manitoba, and Criddle (1928) noted heavy defoliation in western Manitoba in 1911. By 1916, Hewitt (1917b, p. 13) stated that the insect was prevalent in northern Manitoba. According to Lejeune (1947), a second outbreak occurred from 1924 to 1928 and the next recorded infestation began in 1938. By 1946, MacNay (1947) reported that the larch sawfly was the most serious forest pest in the province. The sawfly was first recorded in Saskatchewan by Hewitt (1911, p. 233), in 1910. Twinn (1936) reported an increase in population at Indian Head in 1935, after the cessation of the drought conditions of the previous years. The first authentic record for Alberta is obscure. MacNay (1949) reported the insect from central Alberta in 1948, although, according to Brown (1940), it was present in small numbers in northern Alberta and the Northwest Territories in 1939, and Leech (1944) recorded dead adults in southern Alberta in 1943, presumably from an outbreak in northern Montana.

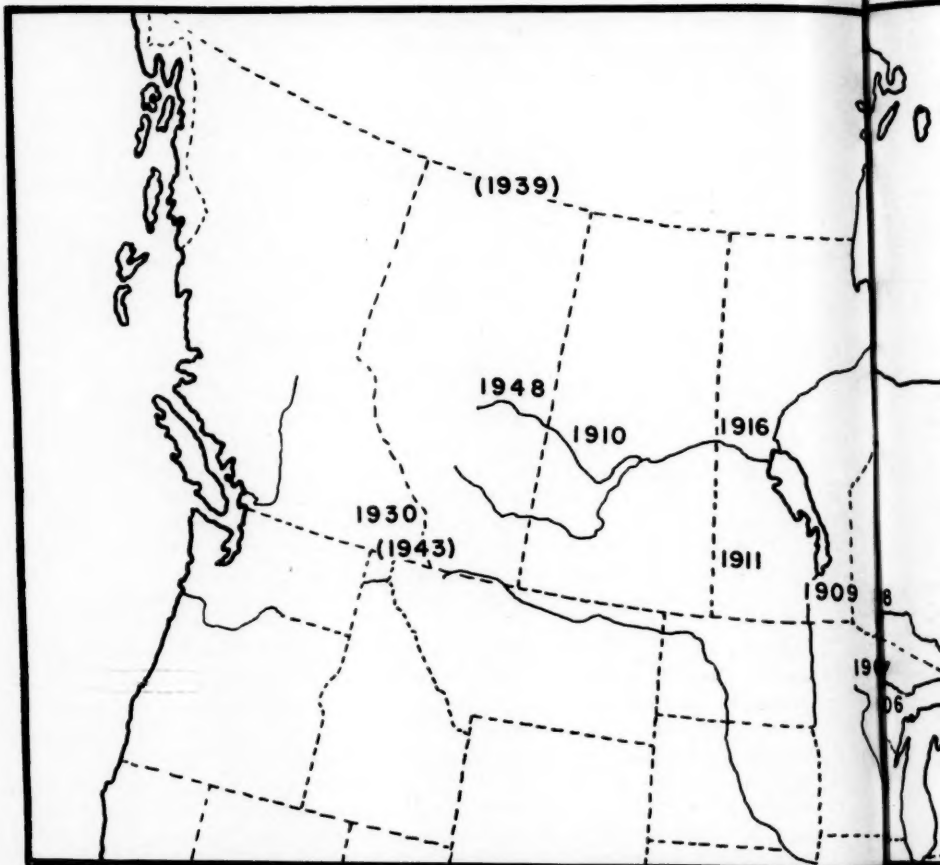


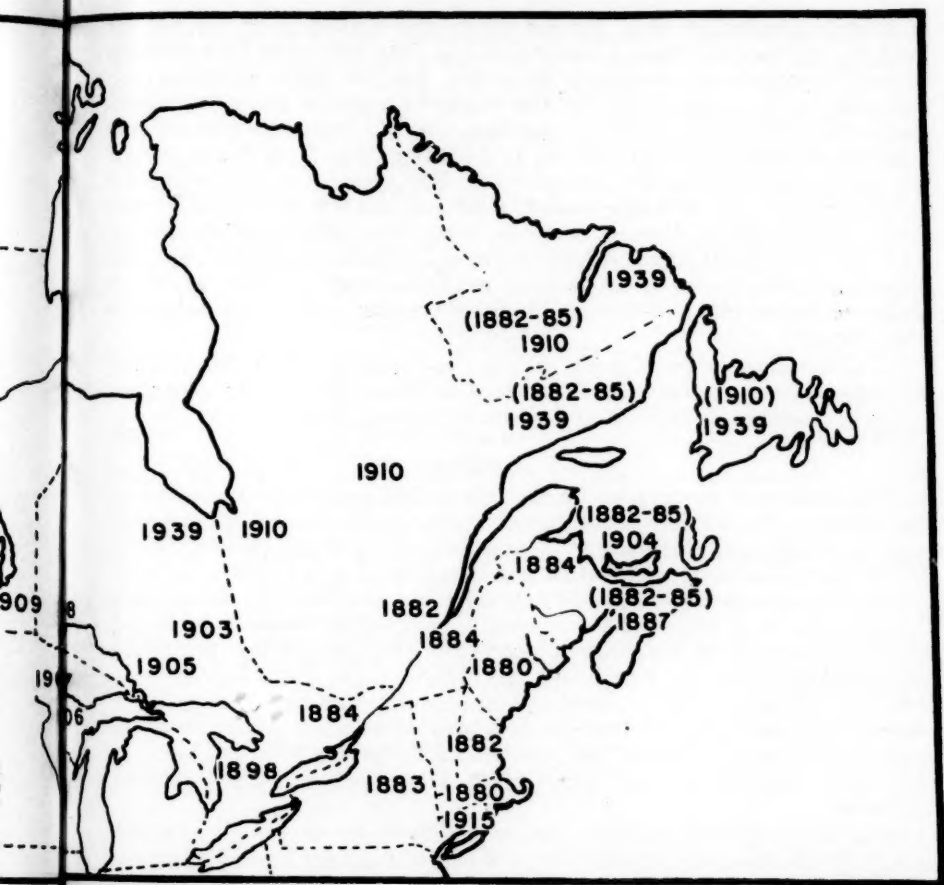
Fig. 1. Dates of earliest records of *P. erichsonii* in Canada and the United States in past

In British Columbia the first record was obtained in 1930 from the Elk River and Fernie areas (Hopping, Leech, and Morgan, 1943). By 1942, it was found at Vernon, the western Canadian limit of *Larix occidentalis* Nutt.

This review of the early records and infestations in the Holarctic region shows that the larch sawfly was present in Europe and North America early in the 19th century. From 1880, reports from North America and Europe were paralleling one another, and since that time infestations on the two continents have coincided rather closely. The current infestations in North America do not appear, however, to have had their counterpart in Palearctic countries, although small outbreaks were reported from Wales in 1948 and England in 1951-52. At the present time, the insect is not numerous in Great Britain or on the continent.

Notes on Origin

In reviewing the possible sources of origin of the larch sawfly, consideration must first be given to its food trees, species of the genus *Larix*. In all, there are



United States in parentheses refer only to dubious or casual references in the literature).

four possible sources, namely: continental Europe, on *Larix decidua* Mill.; Japan, on *Larix leptolepis* (Sieb. and Zucc.) Gord.; Siberia, on *Larix sibirica* Ledeb.; and North America, on *Larix laricina* (Du Roi) K. Koch. This much is known: larch sawflies, similar but not necessarily identical, occur in all these areas. The one country into which this insect certainly has been introduced is England; no native larches existed in England and importations for plantations were made toward the end of the 18th century.

On the origin of the sawfly in North America there are two schools of thought, namely, that the pest has been introduced from Europe and that it is native. According to Graham (1952, p. 214), Packard and Felt assumed that the sawfly was introduced prior to 1880. It first appeared in the eastern United States and was subsequently taken farther west, and tamaracks of large size were apparently common throughout the swamp areas before 1880, the year of the first appearance of the sawfly. In addition, the rapidity with which the parasite *M. tenthredinis*, introduced from England, established itself as an effective agent

of control supports the view that the species was introduced at one time or another. On the other hand, Graham (1952, p. 214) and others have provided evidence in support of the sawfly being native. Detailed studies of annual rings indicated periods of reduced growth that cannot be explained either by suppression or by unfavourable weather conditions. In all, four periods of reduced growth were found: 1835-40, 1850-60, 1870-85, and 1906-15. It is also possible that the pest, or any extensive damage it may have caused, escaped notice since the tamarack swamps held little interest in the early days of the country. The earliest reports such as those by Audubon (1926 [first printing, 1834], pp. 204-205) and Jack (1887) in the United States and Canada respectively indicated defoliation of the larches (most likely by the larch sawfly) as early as 1807 in Maine and in the 1850's in Canada. Audubon's report predates any references from Europe.

The foregoing evidence, going back to the beginning of the 19th century, indicates only that the larch sawfly has been in North America for some time. Its origin cannot be determined on the basis of evidence at hand.

Review of Biology

The biology of the larch sawfly has been studied intensively in many countries; however, the findings of the various workers show considerable variation. Packard (1883) stated that four larval instars occur in America. Hewitt (1912) showed that six larval instars occurred in England, and five in Canada. In interpreting Hewitt's findings, Miles (1936) suggested that Hewitt's larvae from Canada might have been males and those from England females. In Russia, Levteiev (1914) indicated six instars; Dobrodeiev (1921) stated that five occur; and Polyakov (1928), in Siberia, not less than five. In the following year, however, Dobrodeiev (1922) stated that there were six instars. Baird (1923) observed five instars in the Maritime Provinces of Canada. At the Belleville laboratory, in 1954, five instars were observed on the basis of Dyar's formula for larvae both from England and from Canada reared singly and under identical conditions.

The sawfly is thelytokous. Hewitt (1912) never observed copulation during his extensive investigations. At the Belleville laboratory, mating was twice observed in the laboratory, but the transfer to and storage of sperm in the female was not confirmed. Histological examination of male organs indicated that an abundance of sperm is produced.

The sex ratio apparently varies from 0.37 per cent males in England (Hewitt, 1912) through 2.5 per cent males in Manitoba and Saskatchewan, Canada (from rearing at the Belleville laboratory), to some 4 per cent males in eastern and central United States (Graham, 1952, p. 51; Marlatt, 1929, p. 30).

Studies on the biology of sawflies from England and Canada reared at the Belleville laboratory in 1954 have disclosed no marked differences such as those that contributed to Reeks' (1941) separation of the European spruce sawflies.

Notes on Morphological Studies

Large series of pinned specimens from Great Britain and from different regions in Canada were studied intensively at the Belleville laboratory. The English population was found to be homogeneous, suggesting a response of an originally uniform population to a minimum of environmental differences. The specimens from the different regions in Canada demonstrated a greater range of variation, possibly the result of selective adaptation to their environment. The specimens found in Canada show morphological differences from the British

population but the stability of the characters disclosed requires further investigation. The chief areas explored have included the median fovea, the ovipositor sheath, antennae, wings, lancets, and colour pattern.

References

- André, E. 1879-1882. Species des hyménoptères d'Europe et d'Algérie. 1. 644 pp. *Beaune, Côte-d'Or*.
- Audubon, J. J. 1926. Delineations of American scenery and character. [3rd printing] G. A. Baker and Co., N.Y.
- Baird, A. B. 1923. Some notes on the natural control of the larch sawfly and larch case bearer in New Brunswick in 1922. *Proc. Acadian Ent. Soc.* 8: 158-171.
- Balch, R. E., W. A. Reeks, and S. G. Smith. 1941. Separation of the European spruce sawfly in America from *Gilpinia polytomum* (Htg.) (Diprionidae, Hymenoptera) and evidence of its introduction. *Canadian Ent.* 73: 198-203.
- Benson, R. B. 1950. An introduction to the natural history of British sawflies (Hymenoptera Symphyta). *Trans. Soc. Brit. Ent.* 10: 45-182.
- Berland, L. 1947. Hyménoptères Tenthredinoïdes. Faune de France 47. 496 pp. *P. Lechevalier, Paris*.
- Bethune, C. J. S. 1909. Injurious insects in Ontario in 1908. *39th Ann. Rept. Ent. Soc. Ontario*, 1908, pp. 128-135.
- Britton, W. E. 1916. Fifteenth report of the State Entomologist of Connecticut. In Thirty-ninth annual report of the Connecticut Agricultural Experiment Station, 1915, pp. 81-192.
- Brown, A. W. A. 1939. The Canadian forest insect survey in 1939. *70th Ann. Rept. Ent. Soc. Ontario*, 1939, pp. 95-114.
- Brown, A. W. A. 1940. Status of forest insects in 1939. In Annual report of the forest insect survey, 1939, pp. 7-37. *Canada, Dept. Agr., Ottawa*.
- Cameron, P. 1885. A monograph of the British phytophagous Hymenoptera. 2. 233 pp. *The Ray Society, London*.
- Cresson, E. T. 1880. Description of new North American Hymenoptera in the collection of the Entomological Society. *Trans. Am. Ent. Soc.* 8: 7.
- Cresson, E. T. 1887. Synopsis of the families and genera of the Hymenoptera of America, north of Mexico. *Trans. Am. Ent. Soc., Suppl. to Vol. 14*. 350 pp.
- Criddle, N. 1928. The introduction and establishment of the larch sawfly parasite *Mesoleius tentobredinis* Morley, into southern Manitoba (Hymen.). *Canadian Ent.* 60: 51-53.
- Dobrodeiev, A. I. 1921. Bolshoi Listvennitsknoi Pilishtskik [In Russian]. In Reports of the Applied Entomological Section of the Agricultural Research Committee, 1, pp. 100-128. *Peterburg, Russia*.
- Dobrodeiev, A. I. 1922. The large larch sawfly (*Nematus erichsonii* Hartig) and its damage [In English]. In Reports of the Bureau of Applied Entomology of Agricultural Scientific Committee, 2, pp. 168-173. *Petrograd, Russia*.
- Enslin, E. 1912-1918. Die Tenthredinoidea Mitteleuropas. *Beib. Deut. Ent. Z.*, 1912-1917. 790 pp.
- Escherich, K. 1942. Die Forstinsekten Mitteleuropas Hymenoptera (Hautflügler) und Diptera (Zweiflügler). 5. 746 pp. *Carl Parey, Berlin*.
- Fletcher, J. 1885. The larch sawfly—*Nematus erichsonii* Hartig). *15th Ann. Rept. Ent. Soc. Ontario*, 1884, pp. 72-77.
- Fletcher, J. 1888. Report of the Entomologist and Botanist, 1887. In Appendix to the report of the Minister of Agriculture on experimental farms, pp. 8-41. *Canada, Dept. Agr., Ottawa*.
- Fletcher, J. 1893. Report of the Entomologist and Botanist, 1892. In Appendix to the report of the Minister of Agriculture on experimental farms, pp. 144-167. *Canada, Dept. Agr., Ottawa*.
- Fletcher, J. 1906. Report of the Entomologist and Botanist, 1905. In Appendix to the report of the Minister of Agriculture on experimental farms, pp. 159-204. *Canada, Dept. Agr., Ottawa*.
- Fyles, T. W. 1884. Discussion on miscellaneous entomological subjects. *14th Ann. Rept. Ent. Soc. Ontario*, 1883, p. 17.
- Fyles, T. W. 1907. In the tracks of *Nematus erichsonii* Hartig. *37th Ann. Rept. Ent. Soc. Ontario*, 1906, pp. 105-106.
- Graham, S. A. 1952. Forest entomology. *McGraw-Hill Book Co. Inc., New York, Toronto, London*.
- Hagen, H. A. 1881. Entomological notes. *Canadian Ent.* 13: 37.
- Hartig, T. 1837. Die Familien der Blattwespen und Holzwespen nebst einer allgemeinen Einleitung zur Naturgeschichte der Hymenopteren. *Berlin*. 416 pp.

- Hewitt, C. G. 1910. The large larch sawfly. (*Nematus erichsonii*, Hartig). 40th Ann. Rept. Ent. Soc. Ontario, 1909, pp. 20-21.
- Hewitt, C. G. 1910. The large larch sawfly. (*Nematus erichsonii*, Hartig). 40th Ann. report of the Minister of Agriculture on experimental farms, pp. 207-235. Canada, Dept. Agr., Ottawa.
- Hewitt, C. G. 1912. The large larch sawfly (*Nematus erichsonii*) with an account of its parasites, other natural enemies and means of control. Canada, Dept. Agr., Ent. Bull. 5. 42 pp.
- Hewitt, C. G. 1917a. Report of the Dominion Entomologist for the year ending March 31, 1916. Canada, Dept. Agr., Ottawa.
- Hewitt, C. G. 1917b. Report of the Dominion Entomologist for the year ending March 31, 1917. Canada, Dept. Agr., Ottawa.
- Hopping, G. R., H. B. Leech, and C. V. G. Morgan. 1943. The larch sawfly, *Pristiphora erichsonii* (Hartig) in British Columbia, with special reference to the cocoon parasites, *Mesoleius tentbredinis* Morley and *Tritoneptis klugii* (Ratzeburg). Sci. Agr. 24: 53-63.
- Hutt, H. L. 1899. A few of the most troublesome insects of the past season. 29th Ann. Rept. Ent. Soc. Ontario, 1898, pp. 93-97.
- Jack, J. G. 1887. Notes of 1885 on some injurious and other common insects. 17th Ann. Rept. Ent. Soc. Ontario, 1886, pp. 16-17.
- Jarvis, T. D. 1904. Notes on injurious insects of the Abitibi region. 34th Ann. Rept. Ent. Soc. Ontario, 1903, pp. 100-101.
- Konow, F. W. 1890. Tenthredinidae Europae. Deutsche Ent. Z. 1890, pp. 225-255.
- Konow, F. W. 1904. Revision der Nematiden-Gattung *Lygaeonematus* Knw. Z. Syst. Hymen. Dipt. 4: 193-208, 248-259.
- Konow, F. W. 1905. Hymenoptera, Fam. Tenthredinidae. In Genera insectorum, Fasc. 29. 176 pp. P. Wytsman, Bruxelles.
- Leech, H. B. 1944. Summary report of the forest insect survey, British Columbia and Rocky Mountain national parks. In Annual report of the forest insect survey, 1943, pp. 1-70. Canada, Dept. Agr., Ottawa.
- Lejeune, R. R. 1947. Status of the larch sawfly *Pristiphora erichsonii* Htg. in the Prairie Provinces. Canadian Ent. 79: 130-134.
- Levteiev, V. A. 1914. Nabljudeniya po Biologii Listvennago Pililshchika, Rapsovago Pililshchika i Lukovoi Zvetotshnizo. Materialo po Izutsheniju Vrednoh Nasekomoh Moscovskoi Gubernii [in Russian] V: 94-111.
- Long, H. C. 1913. The large larch sawfly. Gardener's Chronicle 54: 184-185.
- MacDougall, R. S. 1906. The large larch sawfly, (*Nematus erichsoni*). J. Board Agr. 13: 385-394.
- MacDougall, R. S. 1912. The bionomics of *Nematus erichsonii* (Hartig), the large larch sawfly. Nature 89: 52-53.
- MacGillivray, A. D. 1917. Tenthredinoidea. In The Hymenoptera or wasp-like insects of Connecticut. Guide to the insects of Connecticut. Part III. Connecticut Geol. Nat. Hist. Surv. Bull. No. 22 (1916). 824 pp.
- MacNay, C. G. 1947. A summary of the more important insect infestations and occurrences in Canada in 1946. 77th Ann. Rept. Ent. Soc. Ontario, 1946, pp. 46-62.
- MacNay, C. G. 1949. A summary of the more important insect infestations and occurrences in Canada in 1948. 79th Ann. Rept. Ent. Soc. Ontario, 1948, pp. 66-87.
- Marlatt, C. L. 1896. Revision of the Nematinae of North America, a sub-family of leaf-feeding Hymenoptera of the family Tenthredinidae. U.S. Dept. Agr., Div. Ent., Tech. Series No. 3. 135 pp.
- Marlatt, C. L. 1929. Report of the Chief of the Bureau of Entomology, 1929. U.S. Dept. Agr.
- Miles, H. W. 1936. On the biology of certain species of *Holcocneme* Kon. (Hymenoptera-Symphyla). Ann. Appl. Biol. 23: 781-801.
- Muldrew, J. A. 1953. The natural immunity of the larch sawfly (*Pristiphora erichsonii* (Htg.)) to the introduced parasite *Mesoleius tentbredinis* Morley, in Manitoba and Saskatchewan. Can. J. Zool. 31: 313-332.
- Packard, A. S. 1883. The larch sawfly worm. In Report on the causes of destruction of evergreen forests in northern New England and New York. Rept. of the Commissioner of Agr. for the Year 1883, pp. 138-146.
- Packard, A. S. 1890. Insects injurious to forest and shade trees. Fifth Report of the United States Entomological Commission, being a revised and enlarged edition of Bulletin No. 7. U.S. Dept. Agr. 928 pp.
- Polyakov, V. Y. 1928. The large larch sawfly (*Nematus erichsonii* Hrt.) [In Russian]. Trans. Siberian Inst. Agr. and Forestry 9: 199-210.
- Provancher, L'Abbé L. 1886. Le nemate d'Erichson. Nat. Canadien 15 (1885): 45-53.

- Provancher, L'Abbé L. 1889. Additions et corrections à la faune hyménoptérologique de la Province de Québec. *Faune Ent. Canada* 2(1885): 5-6.
- Ratzeburg, J. T. C. 1844. Die Forst-Insecten. 3. *Nicolaische Buchhandlung, Berlin*. 314 pp.
- Reeks, W. A. 1941. On the taxonomic status of *Gilpinia polytoma* (Htg.) and *G. hercyniae* (Htg.) (Hymenoptera, Diprionidae). *Canadian Ent.* 73: 177-188.
- Ross, W. A., and L. Caesar. 1932. Insects of the season 1931 in Ontario. *62nd Ann. Rept. Ent. Soc. Ontario*, 1931, pp. 7-14.
- Ross, H. H. 1937. A generic classification of the Nearctic sawflies (Hymenoptera, Symphyta). *Illinois Biol. Monographs* 15. 173 pp.
- Ruggles, A. G. 1911. The larch sawfly in Minnesota. *J. Econ. Ent.* 4: 171-172.
- Thielmann, K. 1939. Die Nematiden der Larche, eine bionomisch, ökologisch forstwirtschaftliche Untersuchung. *Z. Ang. Ent.* 25: 169-214.
- Twinn, C. R. 1936. A summary of insect conditions in Canada in 1935. *66th Ann. Rept. Ent. Soc. Ontario*, 1935, pp. 80-95.

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Population Ecology of the Larch Sawfly¹

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The study of populations and population trends of a forest insect embraces a wide field of activity. By implication, it includes a consideration of all mortality and survival factors. Therefore, in developing this portion of the symposium, it will be necessary to refer briefly to other related topics to be covered later. In addition, to obtain a proper understanding of the subject under discussion, the mode of operation of some population influences that will not be introduced by other members of the symposium will have to be described.

This analysis will be restricted to the larch sawfly and mainly to work done by research officers at the Forest Biology Laboratory at Winnipeg. This is done with the full understanding that important work on the ecology of the larch sawfly and other sawflies is in progress elsewhere in Canada and in the United States.

Life History of Larch Sawfly

To those who are not familiar with the insect, a brief review of its life history should prove helpful. The larch sawfly feeds only on larches. In North America, east of the Rocky Mountains, sporadic, serious outbreaks have occurred on larch or, more correctly, tamarack, *Larix laricina* (Du Roi) K. Koch. The host tree is confined chiefly to swamps. It will be seen subsequently that the physical conditions associated with this habitat impose severe restrictions on sawfly development and survival.

The sawfly adults emerge during May, June, and July, and oviposit in the new terminal shoots of larch. The larvae, upon hatching, feed on the foliage produced as needle clusters on the older twigs. When fully grown, they drop to the ground, burrow into moss or duff, and spin tough, brown, parchment-like cocoons, in which they pass the winter. The main period of larval drop is during July and August. Most larvae resume development in May or June of the following year and transform to pupae and adults within the cocoon. A number of cocooned larvae may, however, remain in diapause for two or more years.

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Development of Program at Winnipeg

At Winnipeg, a research group has developed an intensive program of investigation of the larch sawfly during the past seven years. The program began to take shape about 1948 and has gradually increased in scope and intensity as trained research officers became available.

The initial approach to the problem involved detailed investigations of the more important individual mortality factors. These have been studied experimentally under both field and laboratory conditions wherever possible. Within the last two or three years, a conscious effort has been made to integrate results more closely by consolidating study plots and coordinating projects.

Review of Principal Mortality Factors

Before describing how the various natural controls interact, and how results from several research projects are being integrated, we should consider what is known about individual causes of mortality.

Parasites, predators, and disease are one group of factors obviously entitled to much attention, since, as Dr. Coppel has stated, we are possibly dealing with an introduced insect that may not have the same complement of parasites, predators, and diseases that occurs in Europe. The work on sawfly diseases and that on parasites and predators will be covered by other contributors to this symposium.

In the early stages of our work, it became apparent that water levels were an important environmental influence. Since the host tree normally grows in boggy areas and the sawfly spends about 10 months each year in a cocoon in the ground, the insect is exposed to a wide range of moisture conditions; these may vary from very dry to complete flooding of the cocooning site for long periods. The influence of water levels on development and mortality was studied under controlled field and laboratory conditions. It was found (Lejeune *et al*, 1954) that larvae in newly spun cocoons may succumb if submerged for one or two weeks in late summer. Resistance to flooding increases with aging of the cocooned larvae and their entrance into diapause. In the late fall and early spring, the larvae within cocoons tolerate immersion for several weeks. Resistance decreases as the insect resumes development within the cocoon in late spring and early summer, so that immersion for only a few days causes heavy mortality.

As the progress of infestations was followed, it was noted that the growth responses of the host tree appeared to have an important bearing on population trends. The reactions of larch trees to sawfly defoliation are not completely understood, but they are receiving attention at Sault Ste. Marie (Wallace, 1954), in Minnesota, and at Winnipeg (Heron, 1953). Tree responses introduce elements of competition both for oviposition sites and foliage that can lead to marked declines and fluctuations in populations of the larch sawfly.

Continued severe defoliation causes a progressive reduction in both the number and length of shoots available for oviposition and in the amount of foliage produced annually. As a rule, it is only in the final stages of a prolonged infestation that the scarcity of new shoots may be a limiting factor in the maintenance or survival of sawfly populations. The amount of foliage produced often places a limit on the potential population. Where this is the case, the potential oviposition sites are capable of providing larval populations whose food requirements exceed the quantity of foliage necessary to allow them to complete development. Such conditions may occur in newly infested stands and stands in the intermediate stages of declining vigour (whether caused by defoliation or site conditions). In these stands larval competition for food introduces

additional direct and indirect mortality factors and reduction in reproductive potential.

Last-instar larvae that are unable to satisfy at least half their normal foliage requirement, due to competition for food, suffer heavy mortality (Heron, 1950). The small percentage that do survive, when compared with fully fed controls, show a deficit of over one-half in dry weight and three-quarters in lipid content (Heron, unpub.). In field populations, larvae dropping after defoliation has reached or exceeded 90 per cent showed significant weight losses due to starvation. There is a corresponding reduction in the weight of adults that develop from starved larvae and hence in their fecundity, since there is a direct correlation between adult weight and number of mature oocytes, as determined by dissection (Heron, unpub.).

Interaction of Mortality Factors

A thorough knowledge of the operation of individual mortality factors is essential in studying population trends. However, these factors do not operate independently. Variations in one may set off a sequence of events that produces changes in the intensity of others. An example will help to explain what is meant. Though this illustration is greatly simplified and somewhat hypothetical, the reactions described are based on experimental evidence and observation.

High water levels during the time larvae drop from the trees to spin cocoons may result in the following sequence:

1. Almost complete mortality of larvae that drop into open water.
2. The survivors will spin cocoons in the higher locations, such as hummocks and around the higher roots.
3. The cocoons in the higher locations are more accessible to small-mammal predators, and therefore the percentage of small-mammal predation should be greater. This is being borne out by comparison of predation between wet and dry sites. On the whole, within limits, the effect of high water levels on small mammals appears favourable from the standpoint of larch sawfly control, especially by encouraging the occupancy of the habitat by the more effective *Sorex* group. Furthermore, since some species of mice and shrews appear to have some ability to discriminate between sound cocoons, on the one hand, and diseased cocoons and those parasitized by *Bessa harveyi* (Tsnd.), on the other hand, the loss to the sawfly population is further intensified by the small-mammal predation.
4. Since the ground on the higher sites will warm up more quickly (Turnock, unpub.) the following spring, sawfly adults should emerge earlier than they would from a more randomly distributed cocoon population.
5. The early emerging adults may appear and die before the new terminal shoots are of sufficient length for oviposition.

The sequence of reactions described may be largely reversed if the ground litter is dry during the cocooning period. The larvae will burrow more deeply to spin cocoons or select lower sites; they will not be found so readily by small mammals; and the mean emergence date may be later in the following spring. Some of the apparent advantages to the sawfly derived from a dryer cocooning period may, however, be offset by the increased risk of flooding at the lower cocooning depth later in the summer or in the following spring.

Integration of Mortality Factors

The above account by no means exhausts all the possible interactions. For example, it does not take into consideration the influence of water levels on the host tree, on other soil predators, such as wireworm larvae, on parasites, and on

disease organisms. But it serves to illustrate the complexity of the various interactions. A proper perspective of the true role of the individual mortality factors can only be obtained by some system of integration. The most promising approach appears to be in the use of life tables, such as have been developed for the spruce budworm by Morris and Miller (1954).

Life Table Concept

The approach involves the study of population and mortality factors, with the object of developing life tables for each generation. The successive stages in the life cycle are sampled (stages being referred to as life intervals) and an attempt is made to assign a numerical value to individual, or groups of, mortality factors. The aim in the spruce budworm studies is to prepare life tables for each succeeding generation of the budworm through the rise and fall of an outbreak. The table for one generation should be arithmetically continuous with those for preceding and following generations. It is self evident that the value of a life table is commensurate with the reliability of sampling techniques used to assess (1) population levels at successive life intervals and (2) the kind and incidence of mortality factors.

Population estimates should be expressed on an absolute basis and in terms of a common unit. In this respect, the task of preparing life tables for the spruce budworm is simpler than for the larch sawfly. All the life stages of the spruce budworm normally occur on one universe, the tree, whereas with the larch sawfly, and most other sawflies, there are both tree-inhabiting and ground-inhabiting stages. Theoretically, reliable sampling methods can be formulated for the two universes but the main problem is to express data from the two on a common basis. For the larch sawfly, populations may have to be expressed on an area basis, but to date we have been attempting to express them on a per tree basis.

In one important respect, it is simpler to study the larch sawfly and other sawfly populations than spruce budworm populations. The spruce budworm has three periods of dispersal: during the adult stage; as first-instar larvae before hibernation; and as second-instar larvae after emergence from their hibernacula in the spring. Population gains or losses through dispersal are difficult to assess, as they must be based on addition to or subtraction from the sampling universe, as indicated by population counts, after taking into account other mortality factors. Dispersal of the larch sawfly is limited to the adult stage and, though little is known of the adult flight range, there is no evidence to suggest the occurrence of mass flights of sawfly adults comparable to the recorded mass convectional movements of spruce budworm moths.

Larch Sawfly Life Tables

In 1954, a start was made at Winnipeg in the development of life tables for the larch sawfly. A "pilot" project was set up to develop and assess techniques. Results to date are incomplete and of a preliminary nature but the following discussion outlines how life-table data are being obtained.

The first step is the selection of a study plot. Plot data will comprise a complete tree tally and records on vegetation, topography, and site. Phenological records are essential, since the relation between host tree development and insect development may influence population trends.

Following the selection and establishment of the plot, a number of representative trees (15 in the pilot project) are chosen for carrying out population sampling. The various life stages are then sampled as follows:

1. The initial egg population is determined from a six-branch sample taken from each marked tree in later summer, after seasonal development is completed. It will be recalled that eggs are laid in slits cut into the terminal shoots; the number of eggs laid can be determined by counting egg scars.

2. Egg and early larval mortality is estimated by relating egg scars on selected terminal shoots to the number of first-instar larvae found near the shoot shortly after eclosion. During the first four instars, the larvae are gregarious. They commence feeding below the terminal shoot in which the eggs were laid, and it is therefore possible to relate first-instar colonies to eggs laid.

3. Some indication of the various larval mortality factors and their incidence is being obtained by observing marked larval colonies. Colonies can usually be watched without too much difficulty, as they normally constitute discrete units to the end of the penultimate larval instar, except when populations are high.

4. The number of fully grown larvae that drop to the ground to cocoon is determined by the use of cloth funnels, or drop trays, two under each tree, each covering a sector one-sixth of the area under the crown from the trunk to the foliage perimeter. The percentage parasitized by *Mesoleius tenthredinis* Morley and *B. harveyi* is determined by dissection of samples of larvae taken from the drop trays. The trays may also provide information on mortality from starvation, by comparing survival between partly and completely defoliated trees.

5. Following completion of larval drop, two sectors of the ground under each tree that were not covered by drop trays are sampled to estimate the initial cocoon population before predation of cocoons by small mammals begins. The difference between number of larvae caught in the drop trays and the initial cocoon count gives an estimate of larval loss, before cocooning, caused by small-mammal predation, other predation, flooding, disease, and possibly other factors. A complication in making cocoon counts is that new and old cocoons cannot be differentiated with accuracy.

6. An estimate of cocoon mortality by small mammals and other factors is then derived by means of cocoons planted in the ground. These are examined periodically and followed through to emergence of sawfly adults in the following spring, to provide an over-all estimate of cocoon mortality.

There is the danger that planted cocoons may not be distributed in the same manner as the natural field population. To guard against gross errors in estimates of cocoon losses based on planted material, it is proposed to estimate adult emergence by means of special cages placed on the ground in undisturbed sectors of the sample trees. It may also prove feasible to make a cocoon count in undisturbed sectors in the spring before adults begin to emerge.

At this point complications are introduced by overlapping and interference of several biological control factors acting against cocoons.

If small-mammal predators selected cocoons randomly, the proportion of the population removed by parasites could be determined quite simply. The percentage parasitism of larvae caught in the drop trays could be determined by dissection, and it could then be assumed that the same percentage of cocoons remaining after small-mammal predation was completed would be parasitised. However, there is evidence to suggest that some species of small mammals may be able to discriminate against cocoons parasitised by *B. harveyi* and diseased cocoons. This may cause the incidence of parasitised and diseased cocoons to rise in the residual population as small-mammal predation increases. The interaction of these factors is being studied, though data obtained are still not sufficient to be conclusive. Possibly the net loss to the sawfly population from diseased

larvae in cocoons and parasites can be determined most simply and accurately by examining spring collections of cocoons, after the mammalian predators have completed operations.

An additional complication to be considered is that a percentage of *B. harveyi* larvae emerge from the host larvae shortly after they cocoon. These will not be consumed by small mammals in any case and must be considered separately in our calculations.

7. The number of eggs laid by the sawfly is not easy to establish. A wide variation in number of eggs laid has been obtained from caged females in Minnesota, Manitoba, and Saskatchewan. Some of this variation may be introduced by partial starvation of larvae or by the method of handling the females. Work in progress (Heron, unpub.) indicates that an index of fecundity may be obtained by weighing adults or larvae in cocoons. Even then, it will still be extremely difficult to measure what, in effect, amounts to mortality of adults through lack of suitable oviposition sites, or paucity of oviposition sites caused by loss of tree vigour.

The main problems in securing acceptable life-table data for the larch sawfly are to obtain reliable estimates of (a) cocoon populations, (b) adult emergence, and (c) egg laying. Cocoon sampling presents a particular problem because of the variable topography of larch swamps, which results in a non-random distribution of cocoons. Measurement of adult populations in the field, the number laying eggs, and the number of eggs laid per female, at present, appear as basic weaknesses in most life-table studies. Estimates are usually derived indirectly by relating data on adult emergence, counts of the number of eggs laid in the field, and some index of fecundity based on caged females or some other criteria.

Assuming that sampling difficulties can be overcome, population data obtained for the larch sawfly, when combined into life tables, should provide a picture of mortality and the incidence of most mortality factors during the various life stages. The aim of the sampling and observational techniques will be to reduce to the smallest possible margin of error estimates of mortality attributed to unknown causes.

Value of Life Tables

The paper by Morris and Miller (1954), previously referred to, contains an enlightening discussion on the value of life tables. It states that; "to the practical biologist life tables will be valuable only in so far as they further the understanding of the fundamental epidemiology of the species and aid in the development of control measures. . . . A life table for one generation of the insect in one environment is unlikely to be very helpful in this respect. . . .". It continues; "More valuable information can be shown, however, by continuous life tables for many generations and for different environments." The influence of changes, not only in density but in climatic conditions and environment, should be revealed by life tables.

In the case of the spruce budworm, it is hoped that the accumulation of life tables will provide new and useful information on factors influencing epidemiology, with respect to degree of influence and stage affected. By comparing life tables for various environments and years, information on the effect on population trends, of staminate flower production, stand density and composition, chemical control operations, weather, and parasites, predators, and disease should be obtained.

In general, the same objectives could apply to the larch sawfly, with possibly greater emphasis being placed on measuring the effect of biological control factors, especially if new factors are eventually introduced into North America. Furthermore, life table data may disclose that values now assigned to various natural control factors might have to be revised. Some may be more, or less, important than is supposed on the basis of studies of individual influences. The presence of unsuspected mortality factors might be disclosed. Present knowledge indicates that the most important natural controls of the larch sawfly in Central Canada are: (a) small mammals; (b) *B. harveyi*; (c) flooding; and (d) probably reduced oviposition sites and food sources as a consequence of previous defoliation. However, the importance of these is overshadowed by the marked decline in effectiveness of the introduced parasite, *M. tenthredinis*, in Central Canada and the Lake States. This condition is described by J. A. Muldrew in the next paper, but in considering the epidemiology of the larch sawfly it should be stated that the development of the present outbreak, and its persistence, seems to be related to this phenomenon.

References

- Buckner, C. H. 1954. The role of small mammals as predators of the larch sawfly, *Pristiphora erichsonii* (Htg.), in eastern Manitoba. M.Sc. Thesis. University of Manitoba.
- Heron, R. J. 1950. Starvation of larvae of the larch sawfly. Can. Dept. Agr. For. Insect Invest. Bi-Monthly Prog. Rept. 6(6): 2.
- Heron, R. J. 1953. Substitute shoot production by tamarack. Can. Dept. Agr. For. Biol. Div. Bi-Monthly Prog. Rept. 9(3): 2.
- Lejeune, R. R., W. H. Fell, and D. P. Burbidge. 1955. The effect of flooding on development and survival of the larch sawfly *Pristiphora erichsonii* Hartig (Tenthredinidae). *Ecology* 36: 63-70.
- Morris, R. F., and C. A. Miller. 1954. The development of life tables for the spruce budworm. *Can. J. Zool.* 32: 283-301.
- Wallace, D. R. 1954. Some reactions of larch trees to larch sawfly defoliation. Can. Dept. Agr. For. Biol. Div. Bi-Monthly Prog. Rept. 10(1): 2.

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Parasites and Insect Predators of the Larch Sawfly¹

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Before the introduction of the parasite *Mesoleius tenthredinis* Morley into Canada in 1910, the larch sawfly had periodically caused devastating outbreaks that eventually resulted in the destruction of nearly all the mature larch east of the Rockies. The parasite at first gave control wherever it became established and, following its release in Central Canada, the larch sawfly caused no serious damage there until 1938, when it again began to flare up, first in central Manitoba and then in Saskatchewan, Alberta, Ontario, Minnesota, and Wisconsin. Associated with the present resurgence is a loss of effectiveness on the part of *M. tenthredinis* and this appears to be related to the development of an immunity reaction on the part of the host (Muldrew, 1953a). The larch sawfly in British Columbia is, however, still highly susceptible to the parasite and, apparently, parasitism by *M. tenthredinis* keeps the level of abundance of the larch sawfly so low that difficulty is experienced in obtaining host material for study purposes.

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There is limited evidence that the larch sawfly in Newfoundland is also highly susceptible (Bronskill, 1953, p. 7). The records of the larch sawfly outbreak in the Maritime Provinces from 1933 to 1942 presented by Reeks (1954) show with reasonable certainty that *M. tenthredinis* hastened the end of this outbreak. These records also show that encapsulation of parasite eggs was probably non-existent or was negligible during this period. Studies are now being undertaken to determine whether the current Central Canadian outbreak is actually the result of the appearance into the picture of an immune strain of the larch sawfly.

Unfortunately no data are available on the decline in effectiveness of *M. tenthredinis* in Manitoba between the years 1927 and 1940, but the present state of affairs in British Columbia seems to correspond to the situation that existed in Manitoba in 1927 and perhaps the course of events will be repeated. The situation in British Columbia warrants close scrutiny, since it may reveal the dynamics involved in the spread of physiological races. The further importance of the study of this phenomenon has been pointed out by Dr. C. P. Clausen, Chairman of the Department of Biological Control, University of California (pers. comm.). To his knowledge, this constitutes "the first well-authenticated case of a decline in parasite effectiveness due to the development of resistance by the host." To what extent the phenomenon is comparable to the appearance, in recent years, of strains of insects resistant to certain insecticides is at present unknown, but perhaps studies in British Columbia may clarify this aspect.

Studies on the Immune Strain

An association exists between the property of immunity and the ability of the host larva to deposit a capsule of phagocytic cells around the parasite eggs. In British Columbia a small proportion of the sawfly larvae are resistant and it is in these hosts only that encapsulated eggs have been found. In Central Canadian sawfly larvae, a large majority of the eggs laid by *M. tenthredinis* are encapsulated and only in rare instances have there been indications that parasite larvae hatch from these encapsulated eggs.

M. tenthredinis maintains itself in Central Canada by means of a low hatch in the field. That this breakdown in the resistance mechanism may be due to environmental factors is evidenced by the percentage hatch of eggs being higher in "unhealthy" host larvae and in parasitized larvae reared at low temperatures.

Current work on the immunity reaction at Winnipeg involves: (a) a histological study of the process of capsule formation; (b) investigations on the mechanism and basic causes of the immunity reaction; (c) an attempt to determine the present geographical distribution of the immune strain; and (d) a study to determine if the immunity reaction is heritable. Preliminary work on this last phase is planned in co-operation with Dr. Smith who will comment later on this aspect of the problem. The objective is thus to explain why the parasite has not completely disappeared from the outbreak area, based on the working hypothesis that both immune and susceptible strains of the sawfly coexist in the present outbreak area. It has been postulated that the susceptible strain has superior survival power in the absence of *M. tenthredinis* and begins to supplant the resistant strain when the parasite is at a low density; this in turn leads to an increase in parasite density and a consequent decrease in the susceptible strain, the end result being a kind of self-regulating "feedback system". Smith (1941) in his article on racial segregation states his belief that "the crying need at present is for intensive study to obtain a better understanding of the factors which underlie the struggle for dominance between two or more potential races when subject to the same environmental pressure."

Besides what we have already learned from Dr. Coppel, studies are being conducted at Belleville on the differences in embryological development of *M. tenthredinis* from Western, Central, and Eastern Canada and others are studying the natural control of the larch sawfly in Europe. In co-operation with the Belleville laboratory, an attempt is being made to determine whether the *M. tenthredinis* now present in England differs, with respect to the immunity response of the host, from that now present in Central Canada.

Other Parasites of the Larch Sawfly

In Central Canada, we have at present only two other parasites of the larch sawfly that occur in any numbers; rare occurrences of nine other species have, however, been recorded (Lejeune and Hildahl, 1954). These two are *Tritneptis klugii* (Ratz.) and *Bessa harveyi* (Tsnd.). The former, a pteromalid that parasitizes the cocoon stage, occurs in cocoon collections only sporadically. *B. harveyi*, a tachinid parasite, currently accounts for the highest percentage kill by parasites of the larch sawfly in Central Canada. However, it has never been recorded as parasitizing more than 60 per cent of the cocooned larvae. It builds up slowly in any one local area reaching its maximum density five to eight years after initial appearance but large differences in incidence occur even in closely adjacent infested stands. Hawboldt (1947) has outlined certain mishaps to which it is liable during development. In addition, in Central Canada at least, it appears to be poorly synchronized with its host (Muldrew, 1953b). These phenomena, which reduce its efficiency, may, in part, explain why *B. harveyi* has not exerted any extensive control over the larch sawfly.

Insect Predators of the Larch Sawfly

Insect predators have received only cursory study to date. At least three species of pentatomids, *Apateticus bracteatus* Fitch, *Podisus* sp., and *Euschistus* sp., have been observed feeding on larch sawfly larvae, but they appear of limited value as controlling factors. Elaterid larvae have been found feeding on cocooned larch sawfly larvae, but observations indicate that the conclusion reached by Morris (1951) with respect to the elaterid predators of cocooned larvae of the European spruce sawfly applies here also, namely, that their low percentage kill is attributable to their heterophagous habits and their low rate of food consumption, combined with the failure of their naturally low population level to respond to increasing sawfly populations.

Evidence is accumulating that a considerable proportion of the larch sawfly eggs and first-instar larvae are destroyed by small predators. These include anthocorids, spiders, and mites (Turnock, 1953), and also neuropterous larvae. Wasps have been observed both decapitating and carrying off larvae of the later instars.

Relative Value of Control Factors

It appears that *M. tenthredinis*, in the absence of the resistant strain of larch sawfly, is a "key factor" in the total control complex. It is not known if it would be capable of exerting similar control in the absence of all other mortality factors that operate against its host. However, it does seem that, where *M. tenthredinis* fails to operate at full efficiency, the other mortality factors are capable of control only over limited areas and for restricted periods of time.

In the European spruce sawfly, as Dr. Bird will doubtless relate, we have another example of an insect apparently brought under control by a key factor. This occurred during the period 1938 to 1942; the key factor being a virus disease

that was fortuitously introduced, presumably along with parasite stock obtained from Europe.

The complex of mortality factors acting on each of these two species of sawfly before the appearance of the key factor was roughly the same, namely: small mammals, physical factors, native parasites, and starvation of larvae resulting from their own intense depredations. One difference, however, was that many exotic parasites of the European spruce sawfly had been introduced before the appearance of the disease. The subsequent build-up of these parasites indicated that in the absence of the disease one or more might have become the key factor(s) of control.

It has been suggested that the main difference between such key factors and the less successful factors of control is the sensitivity with which the efficiency of these factors increases with an increase in the density of the host above a threshold level. It is postulated that their density-dependence is more sensitive than that of the less successful factors mainly because they are more specific and have a greater power to infect or to search out the host. The parasite's innate fecundity is thought to be unimportant in this respect especially at low levels of host density.

One of the drawbacks, at present, in the study of density-dependence is that most of what is written and said about this subject is speculation. On the basis of the past performance of certain factors, it is assumed that their efficiency is greatly dependent on the density of the host. Mr. Lejeune, in the foregoing paper, has outlined the life-table study on the larch sawfly that is now being undertaken at the Winnipeg laboratory. This study may enable us to estimate the densities of the larch sawfly and the corresponding densities of certain of the control agents in different areas and over a period of years. From such data it may be possible to obtain estimates of the density-dependence of these agents in quantitative terms. We may then perhaps gain a better understanding of the control effectiveness of each of the members of the total complex of factors that reduce the numbers of this insect.

References

- Bronskill, J. F. 1953. Report of the Biological Control Unit, Can. Dept. Agr., Sci. Ser., Div. of Ent., August.
- Hawboldt, L. S. 1947. *Bessa selecta* (Meigen) (Diptera: Tachinidae) as a parasite of *Gilpinia hercyniae* (Hartig) (Hymenoptera: Diptironidae). *Canad. Ent.* 79: 84-104.
- Lejeune, R. R., and V. Hildahl. 1954. A survey of parasites of the larch sawfly (*Pristiphora erichsonii* (Hartig)) in Manitoba and Saskatchewan. *Canad. Ent.* 86: 337-345.
- Morris, R. F. 1951. The larval Elateridae of eastern spruce forests and their role in the natural control of *Gilpinia hercyniae* (Htg.) (Hymenoptera: Diptironidae). *Canad. Ent.* 83: 133-147.
- Muldrew, J. A. 1953a. The natural immunity of the larch sawfly (*Pristiphora erichsonii* (Htg.)) to the introduced parasite *Mesoleius tentbedinidis* Morley, in Manitoba and Saskatchewan. *Can. J. Zool.* 31: 313-332.
- Muldrew, J. A. 1953b. Population studies on *Bessa harveyi*. Can. Dept. Agr. For. Biol. Div. Bi-Monthly Prog. Rept., 9(3): 2.
- Reeks, W. A. 1954. An outbreak of the larch sawfly (*Pristiphora erichsonii* (Htg.)) in the Maritime Provinces (Hymenoptera: Tenthredinidae) and the role of parasites in its control. *Canad. Ent.* 86: 471-480.
- Smith, H. S. 1941. Racial segregation in insect populations and its significance in applied entomology. *J. Econ. Ent.* 34: 1-13.
- Turnock, W. J. 1953. Some new predators of the larch sawfly. Can. Dept. Agr. For. Biol. Div. Bi-Monthly Prog. Rept. 9(3): 2.

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Small Mammals as Predators of Sawflies¹

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The greatest predatory effect of small mammals is exerted upon insects that spend a portion of their life cycle on the ground or in the soil. Sawflies afford ample opportunity for mammalian predation, since they drop to the ground as mature larvae and spin cocoons in the soil. Such sawflies as *Neodiprion abietis* Harr., which remain within the cocoon for about three weeks, undergo only moderate risk of being preyed upon by small mammals. However, *Pristiphora erichsonii* (Htg.) remains within the cocoon from about mid-August until the following June, or even over more than one year, thus greatly extending the vulnerable period. Earlier investigations suggest that small mammals may comprise the largest single biological control agent acting against this insect (Graham 1928, Lejeune 1951), but the exact role of mammalian predators of forest insects has yet to be established.

Literature Review

Reports of small mammals preying upon forest insects have been published by Hewitt (1912), Graham (1928, 1929), Balch (1939), and Morris (1942, 1949). Graham established that small mammals are very active in searching out and destroying larch sawfly cocoons, and by means of cocoon collections and a cocoon-planting technique it was found that often 50 and occasionally 80-100 per cent of the cocoon population is destroyed by small mammals. Graham also established that cocoons opened by mice could be distinguished from those opened by shrews, and, using this in cocoon analysis, he concluded that mice open many more cocoons than do shrews.

Morris (1949), working with *Diprion hercyniae* (Htg.), further elucidated the role of mammalian predators of forest insects. He pointed out that small mammals had the ability to discriminate between sound and unsound cocoons in varying degrees. This ability, coupled with evidence from cocoon plantings in areas where the shrew population was high, suggested that shrews were more important than was previously supposed. He pointed out, however, that with this insect cocoons opened by mice could not be distinguished from those opened by shrews.

Hamilton and Cook (1940) suggested that were it not for the predatory effect of small mammals many endemic forest insects might soon reach epidemic population levels.

From the literature, it seems evident that two main lines of approach should be considered in establishing the role of small mammals as predators of a forest insect: (1) population trends of both predator and prey species should be studied; (2) the isolated effects, capacities, and habits of the individual predator species should be determined.

Recent Investigations

One characteristic of the larch sawfly is the habitat in which it spins its cocoon. Many sawflies spin cocoons in sandy soil but the larch sawfly normally spins its cocoon in boggy areas. This renders cocoon sampling a difficult, if not

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impossible, task for an individual research worker, and often necessitates the adoption of indirect methods in taking a census of cocoon populations. Where absolute population determinations are required, this may lead to considerable inconvenience. The following discussion illustrates a peculiar problem posed as a result of this characteristic.

In accordance with the logical approaches suggested by earlier work, studies were carried out in southeastern Manitoba to determine in more precise terms the role of small mammals as predators of the larch sawfly. Population-sampling techniques were developed for estimating both predator and prey species. The amount of predation was measured by a modification of Graham's cocoon-planting technique. Populations of cocoons were assessed by collecting the mature larvae in large funnels as they dropped from the trees. Small-mammal populations were measured by means of live traps, utilizing the mark-release-recapture technique (Bailey, 1951). Having a measure of predator and prey populations as an estimate of the predatory effect, the role of mammalian predators can be calculated in terms of cocoons destroyed per mammal per day, and, adding to this the fact that cocoons opened by mice are distinguishable from those opened by shrews, the effectiveness of each of these mammalian orders can be measured. The application of this procedure to data collected in 1952 and 1953 produced conflicting results, since the calculated predation per mammal per day largely exceeded cocoon consumption in cages. It is doubtful whether any individual mouse or shrew could find and open 600 cocoons per day, yet the calculated predation often ranged over 1,000 per day, with one estimate as high as 7,185. Of 55 estimations, 23 were beyond the bounds of credibility.

There are three possible explanations for this apparent discrepancy:—

1. predator population inaccurately measured,
2. predation inaccurately measured,
3. prey population inaccurately measured.

Predator estimates and prey population estimates based on larval-drop counts agreed reasonably well using several techniques. Furthermore, reduction in adult sawfly emergence was directly proportional to predation loss as estimated by cocoon plants. The weakness of the technique appears to be in assuming that the number of larvae dropping provides a reliable estimate of the number of cocoons formed. The data collected suggest that severe mortality of larvae occurs after they have dropped but before they have spun cocoons, and the methods used therefore do not measure the prey population accurately. Larval mortality after dropping could arise from two sources: predation upon the mature larvae by mammalian, avian, and amphibian predators; or losses due to some physical factor, such as an unfavourable moisture relationship. Studies of tethered larvae during 1954 indicate that relatively low numbers of dropped larvae are destroyed by predation. In addition, when the population figure is corrected by estimating those larvae that drowned in surface puddles, the error, although considerably reduced in magnitude, remains inherent in the estimates. However, one salient feature arising from the results is that the error is proportional to the depth of water in the three plots studied. Had direct cocoon sampling been feasible, this problem would not have arisen.

A second characteristic of the larch sawfly that reportedly renders it highly susceptible to small-mammal predation is its prolonged period within the cocoon. Early investigators suggested that the insect is extremely vulnerable, since it remains within the cocoon for almost 10 months of the year. However, the data collected during the present study, using the cocoon-planting technique,

do not support this argument. Predation begins in the field in late August after the larvae have dropped to the ground, reaches a peak in mid-September, and then declines slowly until the ground freezes (Buckner, 1953). This constitutes the entire period of predation upon the larch sawfly, indicating a duration of possibly no more than two months. The chronology of predation is, however, extremely important, for during this period the small-mammal population is at its seasonal peak. Forest insects that emerge before the small-mammal peak miss this optimal predation potential.

A further factor in evaluating the nature of small-mammal predation is the variation in the habitat of the host. The larch sawfly spins cocoons in ground litter ranging from very dry to extremely wet. Accompanying this is a corresponding difference in small mammal complement. *Microtus pennsylvanicus* is the dominant species in dry to moderately wet sites where the crown closure is not great; *Clethrionomys gapperi* in dry to moderately wet sites with a high percentage of crown closure; and *Sorex cinereus* in wet sites with heavy crown closure. Added to these population effects is evidence that these species are able to differentiate between sound, diseased, and possibly parasitized cocoons in varying degrees, thus eliminating to some extent the overlap in biological control factors. Thus, in areas where *S. cinereus* is dominant, predation is not only numerically greater but also more efficient selectively. Additional evidence collected in the latter part of the 1954 season suggests that *Sorex arcticus* consumes sound and parasitized cocoons indiscriminately, but this is somewhat balanced by the higher food capacity of this species. Further information on habitat change will become available over the next few years, since highway engineers recently drained a very wet bog that has been under investigation for the past three years. Already the small-mammal population has changed markedly, for, whereas *S. cinereus* was previously the dominant form, this species is now almost entirely replaced by *S. arcticus*. Undoubtedly additional effects will be exerted upon small-mammal, insect, and host-tree components.

References

- Bailey, N. T. J. 1951. On estimating the size of mobile populations from recapture data. *Biometrika* 38: 293.
- Balch, R. E. 1939. The outbreak of the European spruce sawfly in Canada and some important factors of its bionomics. *J. Econ. Ent.* 32: 412-418.
- Buckner, C. H. 1953. Small mammals as predators of the larch sawfly. Can. Dept. Agr. For. Biol. Div. Bi-Monthly Prog. Rept. 9(6): 2.
- Graham, S. A. 1928. The influence of small mammals and other factors upon the larch sawfly survival. *J. Econ. Ent.* 21: 301-310.
- Graham, S. A. 1929. The larch sawfly as an indicator of mouse abundance. *J. Mammal.* 10: 189-196.
- Hamilton, W. J. Jr., and D. B. Cook. 1940. Small mammals and the forest. *J. For.* 38: 468-473.
- Hewitt, C. G. 1912. The large larch sawfly. Can. Dept. Agr. Expl. Farms Bull. No. 10.—Second Series, Ent. Bull. No. 5: 1-42.
- Lejeune, R. R. 1951. Some ecological factors governing populations of the larch sawfly, *Pristiphora erichsonii* (Htg.). *Canad. Ent.* 83: 152-156.
- Morris, R. F. 1942. Preliminary notes on the natural control of the European spruce sawfly by small mammals. *Canad. Ent.* 74: 197-202.
- Morris, R. F. 1949. Differentiation by small mammal predators between sound and empty cocoons of the European spruce sawfly. *Canad. Ent.* 81: 114-120.

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Virus Diseases of Sawflies¹

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Although a virus disease of the larch sawfly, *Pristiphora erichsonii* (Htg.), has not been discovered, polyhedrosis viruses of several other Tenthredinids are known. They have been used to control infestations of two introduced species: the European spruce sawfly, *Diprion hercyniae* (Htg.), (Bird, 1954) and the European pine sawfly, *Neodiprion sertifer* (Geoffr.), (Bird, 1950, 1952, 1953; Dowden, 1953). Unfortunately, the viruses of these, as well as the viruses of several other species tested, are not pathogenic to the larch sawfly. Some viruses, however, appear to be pathogenic to more than one species. J. M. Burk of this laboratory found, for example, that a polyhedrosis virus affecting the native jackpine sawfly, *Neodiprion americanus banksianae* Roh., is pathogenic to *N. sertifer*, *N. nanulus* Schedl, and *D. hercyniae*.

Use of Viruses in Biological Control

The virus used in the biological control of *N. sertifer* was obtained from Sweden, where, as in other parts of Europe, it is chiefly responsible for controlling outbreaks of this insect. Following experiments in the laboratory and in the field, the virus was made available to growers of Scots pine in southern Ontario and has been distributed to several parts of the United States. In general, it has replaced insecticides in controlling this sawfly. With very dilute aqueous suspensions of the body fluids of virus-killed larvae, entire feeding populations of the insect may be destroyed. However, for reasons to be discussed, it is not advisable to destroy all the insects. Infestations are controlled eventually by epizootics resulting from small introductions of the virus. For example, an infestation extending over 100 acres of Scots pine was controlled in three years by epizootics each year resulting from one introduction of virus in 1951.

Similar results have been obtained using a virus against *D. hercyniae*. This virus has been propagated continuously in the laboratory since 1940 and is the one that controlled outbreaks of the sawfly in Eastern Canada about a decade ago (Balch and Bird, 1944). Apparently it was accidentally introduced into Canada from Europe. The effectiveness of the virus in biological control has been demonstrated in several field tests in the Maritime Provinces and in Ontario. In 1950, three spruce trees infested with *D. hercyniae* were treated with virus in a formerly disease-free, lightly-infested area near Sault Ste. Marie. One year later (during the third sawfly generation) heavy mortality from virus was observed on all trees within 500 ft. of the sprayed trees and diseased larvae were found up to 2,000 ft. from the sprayed area. There was a more rapid spread of virus in heavily forested areas than where trees were isolated one from another.

Not all virus diseases are as effective in controlling insect outbreaks as those discussed above. A virus of the jack-pine sawfly, *N. a. banksianae*, was discovered causing small percentages of mortality towards the end of an outbreak of this insect near Sault Ste. Marie. The virus did not appear to be highly pathogenic nor was it considered an important factor in the control of the sawfly. In 1953 and 1954 the virus was artificially disseminated in a jack-pine sawfly infestation, apparently disease-free, about 200 miles from Sault Ste. Marie. Such heavy suspensions of the virus were necessary to destroy the larvae that it would be

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impractical to aim for mortality in excess of 70 per cent, the scale of virus production necessary for greater control being prohibitive. Moreover, spraying would have to be repeated each year, since epizootics do not result from small introductions of the virus and do not recur year after year even in areas where it has been introduced.

The virus of the jack-pine sawfly was chosen for field studies because of its apparent low-pathogenicity. There is no justification for comparing the effectiveness of this native virus with the introduced viruses of *D. hercyniae* and *N. sertifer*. Although the viruses of the latter two species are effective in control in Europe, recent studies by Franz and Niklas (1954) indicate that outbreaks of *N. sertifer* in Germany could be controlled much earlier by the artificial dissemination of the virus.

Transmission of Viruses

Viruses are transmitted from one year to the next chiefly through eggs of infected adults. Larvae that hatch from infected eggs die at an early stage of development. Little, if any, virus remains on the foliage over winter and survival of part of an infected population is therefore necessary to ensure infection of the progeny of those insects in diapause at the time of the dissemination of the virus and of the progeny of immigrants. Studies of *N. sertifer* have shown epizootics to start from the infection of about 15 per cent of the egg clusters. Similarly, studies of *D. hercyniae* have shown epizootics to start each year from the infection of small percentages of the populations.

Mortality of *N. sertifer* in Scots pine trees depends on the number and position of the colonies infected via the egg and on the population density. The virus spreads more rapidly down the tree, so that an infected colony at a strategic position at the top of a tree causes rapid infection and death of the larvae throughout the tree. There may be no spread of virus from an infected colony in an isolated position at the bottom of the tree. Unless a tree contains a colony infected via the egg, mortality from virus, if it occurs, is usually low and develops late in the season. Trees with less than five colonies of *N. sertifer* (about 300 larvae) rarely contain an infected colony. Plantations of small trees are severely defoliated by less than five colonies per tree. The virus, therefore, gives poor natural protection to young plantations and must be artificially disseminated until the trees are large enough to support higher populations.

The virus of *D. hercyniae* appears to be the more effective at low population levels. This may be due to differences in the habits of the two host species. *D. hercyniae* lays its eggs singly and the larvae feed singly. The progeny of an infected adult may, therefore, establish many foci of infection. *N. sertifer* lays its eggs in one cluster and the larvae feed gregariously. Only one focus of infection is established since the entire colony of some 60 larvae dies at an early stage of development before the tendency to wander begins.

Many factors aid in the transmission of viruses during the growing season (parasitic, predacious, and scavenging insects, birds, etc.). Mortality from virus, initiated through infected eggs, increases rapidly. Only those insects survive that mature, drop to the ground, and spin cocoons before becoming infected with virus or those that become infected with virus late in development and are able to regenerate the cells destroyed by the virus (Bird, 1951). In the cases of *N. sertifer* and *N. a. banksianae* more males than females survive because the males have one less instar and complete their development about a week earlier than the females. *D. hercyniae* reproduces by obligatory parthenogenesis and males are consequently rare. An interesting observation in studies on transmission

of virus by birds was made with my colleague, C. S. Holling of the Forest Insect Laboratory, Sault Ste. Marie. The stomach contents of four birds killed in a Scots pine plantation infested with *N. sertifer* were found to contain remnants of *N. sertifer* larvae. Since most of the insects in the infestation were either infected with or killed by the virus at that time, the stomach contents were stored at 40°F. and later tested for virus activity. The tests were made eight months later by feeding aqueous suspensions of the stomach contents to healthy *N. sertifer* larvae. The stomach contents of the cat-bird and cedar wax wing were highly infectious. It therefore seems probable that viruses are also transmitted through the droppings of birds and may be distributed over long distances.

Epizootiology

Populations of *D. bercyniae* have been studied continuously in New Brunswick for about 18 years, from just before the initial occurrence of mortality from the virus disease. Epizootics reduced populations between 1938 and 1942 to a very low level. The effectiveness of the virus was thereby reduced and as a consequence the numbers of sawflies increased rapidly. Mortality from virus again became evident in the relatively high populations by the latter part of 1944, and severe virus epizootics recurred in 1945. Introduced parasites first became prevalent about this time, and together with the virus, reduced sawfly populations still further. Since 1945, populations have been kept under control chiefly by introduced parasites and, in general, at a level below that at which the virus is an effective control factor.

Whether by good management or good luck, the biological control of *D. bercyniae* was well executed. Parasitic insects were introduced and became established at high host population densities. The immediate threat to the spruce forests was removed by the establishment of the virus disease. The only improvement that possibly could have been made would have been the introduction of the virus early enough to prevent tree mortality, particularly in the Gaspé Peninsula. It is questionable, however, whether an earlier introduction of the virus would have allowed sufficient time for the establishment of the parasites.

The immediate threat to Scots pine in southern Ontario has been removed by the introduction of the virus disease affecting *N. sertifer*. There is no evidence to indicate that well-established native parasites have affected or will affect population trends. The "key factor" is the virus disease, and except in plantations of small trees, adequate control is obtained by recurring virus epizootics.

Factors Affecting the Pathogenicity of Insect Viruses

The effectiveness of highly pathogenic viruses, such as those used in the biological control of *D. bercyniae* and *N. sertifer*, appears to be independent of stress conditions and such secondary factors as kind of food and weather. That secondary factors may be important in increasing the pathogenicity of some viruses is indicated by the work of Yamafugi and Yoshihara (1950), Schwetzwowa (1950), and Vago (1953). Yamafugi and Yoshihara found a higher incidence of disease among silkworm larvae fed potassium nitrite. Schwetzwowa believes that waxmoth larvae (*Galleria mellonella* L.) are most susceptible to virus when fed wax enriched with nitrogen and carbohydrates. Vago found a greater incidence of virus disease among silkworm larvae fed sodium fluoride. According to Vago, certain varieties of mulberry increase the incidence of mortality among silkworm larvae. Similarly, information obtained by Sippell (1952) indicates that more forest tent caterpillars, *Malacosoma disstria* Hbn., die from virus disease

when fed maple. Potassium nitrite and sodium fluoride appear to have no effect on the susceptibility of *D. hercyniae*, *N. sertifer*, or *N. a. banksianae* to virus disease, nor does feeding the insects on different species of spruce or pine.

Larvae of *D. hercyniae* appear equally susceptible to virus when reared under high or low relative humidities but, in general, die more rapidly when reared at high than at low temperatures. Since larval development is similarly affected, larvae fed the same amount of virus die at about the same stage of development regardless of the temperature. In the field, the effect of cold weather is to retard both larval and disease development. Continuous rearing at very high temperatures (85°F.) inhibits virus multiplication, but the larvae die rapidly when transferred to 72°F. or when alternated between 85°F. and 72°F. at 12 or 24-hour intervals.

Insect viruses are capable of maintaining their pathogenicity in storage and in nature over long periods of time. In storage, cadavers of *D. hercyniae* contained infectious material after 14 years. In nature, the virus of *D. hercyniae* appears to be as effective a control factor today as it was 18 years ago. No change is evident in the pathogenicity of *N. sertifer* virus since its introduction into Canada in 1949. It would be unusual, in comparison with virus epidemics of man, if these high pathogenicities were maintained indefinitely.

References

- Balch, R. E., and F. T. Bird. 1944. A virus disease of the European spruce sawfly, *Gilpinia hercyniae* (Htg.) and its place in natural control. *Sci. Agr.* 25: 65-80.
- Bird, F. T. 1950. The dissemination and propagation of a virus disease affecting the European pine sawfly, *Neodiprion sertifer* (Geoffr.). Can. Dept. Agr. Forest Insect Invest. Bi-Monthly Prog. Rept. 6 (5).
- Bird, F. T. 1952. On the artificial dissemination of the virus disease of the European pine sawfly, *Neodiprion sertifer* (Geoffr.). Can. Dept. Agr. For. Biol. Div. Bi-Monthly Prog. Rept. 8 (3).
- Bird, F. T. 1953. The use of a virus disease in the biological control of the European pine sawfly, *Neodiprion sertifer* (Geoffr.). *Canad. Ent.* 85: 437-446.
- Bird, F. T. 1953. The effect of metamorphosis on the multiplication of an insect virus. *Can. J. Zool.*, 31: 300-303.
- Bird, F. T. 1954. The use of a virus disease in the biological control of the European spruce sawfly, *Diprion hercyniae* (Htg.). Can. Dept. Agr. For. Biol. Div. Bi-Monthly Prog. Rept. 10.
- Dowden, P. B., and H. B. Girth. 1953. Use of a virus disease to control European pine sawfly. *J. Econ. Ent.*, 46: 525-526.
- Franz, J., and O. F. Niklas. 1954. Feldversuche zur Bekämpfung der roten Kiefernbuschhornblattwespe (*Neodiprion sertifer* (Geoffr.)) durch Künstliche Verbreitung einer Virusseuche). *Nachr. Deutsch. Pflanzenschutzdienstes.* 6: 131-139.
- Schwetzwowa, O. I. 1950. Die Polyederkrankheit der grossen Wachsmotte (*Galleria mellonella* L.) und die Rolle des Nahrungsfaktors bei den Viruskrankheiten der Insekten. *Mikrobiologia* 19: 532-542.
- Sippell, W. L. 1952. Winter rearing of the forest tent caterpillar, *Malacosoma disstria* Hbn. Can. Dept. Agr. For. Biol. Div. Bi-Monthly Prog. Rept. 8 (4).
- Vago, C. 1953. Essais d'élimination de la grasserie par activation de sa phase latente. *J. Silkworm* 5: 73-81.
- Yamafuji, K., and F. Yoshihara. 1950. On the virus production and oxime formation in silkworms fed with nitrites. *Agr. Chem. Inst., Kyushi Univ., Fukoka, Japan.* 30: 5.

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Fungal and Bacterial Pathogens of the Larch Sawfly¹

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Fungi and bacteria each play a role in the natural control of many sawflies, including *P. erichsonii*. Parasitic fungi, for example, have been isolated from species in the following genera: *Anoplonyx*, *Arge*, *Monoctenus*, *Neodiprion*, *Trichiosoma*, *Hemichroa*, *Pikonema*, and *Pristiphora*. The isolates include species from *Cephalosporium*, *Sorosporella*, *Isaria*, *Beauveria*, *Spicaria*, *Hirsutella*, and *Empusa* (MacLeod, unpub.). The last five fungus genera have been isolated from larch sawfly collections made in various parts of Canada and the United States.

An examination of approximately 16,000 field-collected larvae during the five-year period 1948-1952 showed that the number infected with *Beauveria* strains ranged from 0.2 to 1.5 per cent. Examination of 11,000 cocoons during the same period showed mortalities ranging from 2.8 to 23.5 per cent. Under laboratory conditions, heavy mortality develops within a period of six to ten days when spores of *Beauveria bassiana* (Bals.) Vuill. are sprayed or dusted on larch sawfly larvae. Under field conditions, the artificial dissemination of spores on feeding larvae increased the incidence of *Beauveria* infection from 1.5 to 9.5 per cent. The examination of cocoons that contained larvae sprayed with spores and larvae that had spun up in ground previously sprayed with spores showed mortality due to *Beauveria* infection to range from 2.5 to 30.8 per cent (MacLeod, 1954; Heimpel, unpub.).

Although field tests have not yet been carried out with the remaining fungi, it is known that they too exert some control. Hewitt (1912) found *Isaria farinosa* (Dicks.) Fr. to be an important factor in the control of this species in England, for he found that as many as 25 per cent of the cocoons were attacked under forest conditions in Cumberland.

On the basis of experiments with Hewitt's material, Güssow (1911) concluded that *I. farinosa* is truly parasitic on larch sawfly cocoons and that, due to its otherwise saprophytic mode of existence, little doubt remains that the pupating larvae infect themselves after dropping to the ground.

Cocooned larvae are frequently found infected by a species of *Empusa*. Moreover, among feeding larvae, mortality due to this fungus is usually higher than that attributable to any other fungus and, in many instances, localized populations are known to have suffered heavy mortality. *Empusa* species have in fact been isolated from at least 20 different insect species throughout Canada in the last few years and in many are responsible for heavy loss. Thus it is believed that the green apple bug, *Lygus communis* var. *novascotiensis* Knight, in the Annapolis Valley was being practically held in check by *Empusa erupta* (Dustan, 1924). Similarly, Dustan (1923) and Gilliatt (1925) found that, in orchards where *Entomophthora sphaerosperma* (Fres.) was present, nymphs of the European apple sucker, *Psylla mali* (Schmid.), were so reduced in number that little injury was caused to the trees. Again, during the summer of 1947, a heavy infestation by the pea aphid, *Macrosiphum pisi* Kaltenback, was checked throughout the Annapolis Valley by *Empusa aphidis* Hoffman (MacLeod unpub.).

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Many publications point out that economic control by means of entomogenous fungi is outstanding in areas with abundant rainfall and high mean temperatures, such as Florida. Nevertheless, it is apparent that fungi in general contribute greatly to the total mortality of insects in Canada as well. They are always present and, although perhaps varying in intensity, each is doubtless sufficiently numerous to play a role in natural control.

Billings and Glen (1911) failed to increase mortality among chinch bug nymphs (*Blissus leucopterus* (Say)) through the distribution of additional spores of "*Beauveria globulifera* (Speg.) Pic.". Fawcett (1944) suggested that this was because a "saturation point"⁴ probably exists most of the time due to the abundance of wind-borne spores the fungus is capable of producing, so that no higher mortality is to be expected from adding spores without at the same time changing the conditions. This efficient natural dissemination, which appears to characterize some fungi may, however, not occur so easily with certain entomogenous fungi of more highly specialized parasitism. Both Gilbert (1926) and Tisdale (1930) have pointed out that the natural distribution of the aphid-fungus *Empusa fresenii* Now. in Florida lags far behind the maximum potential degree of infection. It appears to depend for its propagation on spores that are not readily borne by wind at the time of insect migration. It is known that some of the fungi attacking the larch sawfly, for example some strains of *B. bassiana* and species of *Spicaria*, *Hirsutella*, and *Empusa*, do not form spores readily on artificial media and indeed some have never been found sporulating even on their natural hosts. The natural distribution of these fungi may thus lag far behind the possible maximum degree of infection: a saturation point may never be reached. Should, therefore, satisfactory media for the growth and sporulation of these fungi develop out of investigations now in progress, increased infection might well be expected from the artificial dissemination of spores in the field.

Bacteria cause few deaths among feeding larvae of the larch sawfly in Canada. Field surveys, conducted during the years 1949 to 1952 in northwestern Ontario, showed that mortality due to bacteria ranged from 0.6 to 2.0 per cent of some 5200 larvae under close observation. Most deaths were caused by *Bacillus cereus* Fr. and Fr. but several other species of bacteria representing the families *Micrococcaceae*, *Bacteriaceae*, and *Bacillaceae* were isolated. Subsequent feeding tests, using pure cultures of the isolated species, indicated however that only strains of *B. cereus* were virulent for this insect, other species in the insect cadavers being apparently adventitious. *B. cereus* normally occurs in soil and dust, and must be ingested by the insect to bring about infection. One possible explanation of the low natural mortality caused by *B. cereus* in larch sawfly populations is that, the larch tree being an inhabitant of damp sites, there is little chance of dust (with *B. cereus* spores adhering thereto) being blown up onto the foliage.

Overwintering larch sawfly larvae do not appear to suffer from bacterial infection. When, however, dead larvae were found to contain bacteria, culturing almost invariably revealed the presence of several species of bacteria, none of which proved to be virulent when fed to healthy larvae. This is not surprising, for larvae dead from almost any cause inevitably become heavily infested with saprophytic species of bacteria.

Strains of *B. cereus* vary in their ability to kill sawfly larvae. Investigations into the mode of action of *B. cereus* during the process of invasion led to some interesting conclusions that are applicable to the action of this bacterium in insects generally. First, it was found that an enzyme, lecithinase, produced by *B. cereus*

⁴Fawcett (1944) has suggested that the "saturation point" for fungus and insect occurs when the conditions for natural distribution of a fungus are such that there is the maximum possible number of spores capable of infecting the maximum possible number of insects under prevailing environmental conditions.

is in part responsible for its virulence. Second, it was shown that the pH in the larval midgut is an important factor in determining whether spores of *B. cereus* can germinate and whether the vegetative rods and their products of metabolism can overcome the natural resistance of the host and cause death.

Field and laboratory feeding tests of *B. cereus* strains resulted in mortalities up to 38 and 60 per cent respectively (Heimpel, 1954). The survival in these tests is probably due, as in any biological system with two living organisms involved, to variability in host resistance, as well as variability in the virulence of the pathogen. Studies of the inherent resistance of the host insect and the variability of the bacterium are currently being undertaken as a joint project with the Cytogenetics Section of the Forest Insect Laboratory.

It has been found that the larch sawfly's digestive tract and blood do not contain any antibiotic, or inhibitory substances, effective against *B. cereus*.

Other means of preventing invasive action by *B. cereus* are of course possible. Non-susceptible larch sawfly might have abnormally high concentrations of calcium or magnesium ions in their blood, and it is known that high concentrations of these ions are capable of inhibiting toxic lecithinase produced by *B. cereus*.

Recently it was noted that a species of *Enterobacteriaceae*, *Serratia marcescens* Bizio, is relatively pathogenic for the larch sawfly. Other sawflies tested and found to be susceptible are *Neodiprion americanus banksianae* Roh., *Neodiprion lecontei* (Fitch), *Hemichroa crocea* (Fourcroy), and *Nematus ribesii* (Scop.). Monsour and Colmer (1951) discovered that *S. marcescens* produces a lecithinase identified by these investigators as lecithinase C—a choline phosphatase, but it is as yet unknown whether this lecithinase is the virulent agent of *S. marcescens*.

The rapid increase in knowledge of the physiology and genetics of both fungi and bacteria gives promise of success in the experimental production of more virulent pathogens. It is of interest that Lederberg and Tatum (1946), working on bacteria, and Pontecorvo (1947), working on asexual fungi, have shown that genetic factors initially carried in different cells can be combined within one cell. Thus virulent strains of a pathogen might arise following genetic recombination between two or more non-virulent strains. In an epidemic cycle, we may therefore expect a long period during which two or more non-virulent strains spread independently and build up their incidence in a population. When the incidence reaches a level at which double infection of the host species becomes frequent, virulent combination-forms should begin to be produced, soon to be followed by an epidemic outbreak.

References

- Billings, F. C., and P. A. Glenn. 1911. Results of the artificial use of white fungus disease in Kansas. U.S.D.A. Bur. Ent. Bull. 107: 1-58.
- Dustan, A. G. 1923. A fungous parasite of the imported apple sucker (*Psyllia mali* Schmid.). Artificial spread of *Entomophthora sphaerosperma*. Agric. Gaz. Can. 10: 16-19.
- Dustan, A. G. 1924. Studies on a new species of *Empusa* parasitic on the green apple bug (*Lygus communis* var. *novascotiensis* (Knight) in the Annapolis Valley. Proc. Acadian Ent. Soc. 9: 14-36.
- Fawcett, H. S. 1944. Fungus and bacterial diseases of insects as factors in biological control. Bot. Rev. 10: 327-348.
- Gilbert, E. M., and W. A. Kuntz. 1926. Some diseases of *Aphis spiraeicola* Petch. Fla. St. Pl. Bd., Quart. Bull. 10: 1-6.
- Gilliatt, F. C. 1925. Some new and unrecorded notes on the life history of *Entomophthora sphaerosperma*. Proc. Acadian Ent. Soc. 10: 46-54.
- Güssow, H. G. 1911. Observations on the parasitism of *Isaria farinosa* (Dicks.) Fr. with special reference to the larch sawfly (*Nematus erichsonii* Hartig). Trans. Roy. Soc. Can. 3rd series 4: 5-99.

- Heimpel, A. M. 1954. A strain of *Bacillus cereus* Fr. and Fr. pathogenic for the larch sawfly, *Pristiphora erichsonii* (Htg.). *Canad. Ent.* 86: 73-77.
- Hewitt, C. G. 1912. The large larch sawfly (*Nematus erichsonii*). *Can. Dept. Agr. Expl. Farms Bull. No. 10.—Second Series, Ent. Bull. No. 5:* 1-42.
- Lederberg, J., and E. L. Tatum. 1946. Novel genotypes in mixed cultures of biochemical mutants of bacteria. *Cold Spring Harbour Symp. Quant. Biol.* 11: 113-114.
- MacLeod, D. M. 1954. Investigations on the genera *Beauveria* Vuill. and *Tritirachium* Limber. *Can. J. Bot.* 32: 818-890.
- Monsour, V., and A. R. Colmer. 1951. A study of lecithinase activity within the genus *Serratia*. *Bact. Proc.* 63: 57-58.
- Pontocorvo, G. 1947. The origin of virulent strains as recombinants from non-virulent strains, and the kinetics of epidemics. *Proc. 4th Intern. Congr. Microbiol. Copenhagen:* 376.
- Tisdale, W. B. 1930. Diseases of citrus aphids. *Fla. Agr. Exp. Sta., Ann. Dep.:* 96.

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Cytogenetics of Obligatory Parthenogenesis¹

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The larch sawfly, *Pristiphora erichsonii* (Htg.), like the European spruce sawfly, *Diprion* (*Gilpinia*) *hercyniae* (Htg.), is an obligatory parthenogenetic 'species', that is, it is endowed with the capacity of reproducing without recourse to mating. While this absence of cross-fertilization with the attendant uniformity of progeny it assures renders such species ideally suited for experiments requiring the use of controls, it would at first sight appear to preclude the adoption of conventional genetic procedures in studying them, other than by circuitous means: it is the main purpose of this contribution to suggest a possible means of circumventing the difficulty.

That both species have evolved from normal bisexual progenitors is evidenced by their occasional production of males. In bisexual Hymenoptera, males develop from unfertilized eggs: they have only one set of chromosomes and are accordingly haploid. Females, on the other hand, develop from fertilized eggs: they receive one set of chromosomes from each parent and are accordingly diploid. Moreover, all daughters are semi-identical, for their father's sperm are all of one type. Obligatory parthenogenetic females dispense with the need for fertilization either by dispensing with the maturation divisions that reduce the number of chromosomes, or if these divisions occur, by incorporating some secondary mechanism that compensates for the earlier reduction. A number of diverse mechanisms, reducible to two main types, are known by which diploidy is retained or restored: they have profoundly different consequences when measured in terms of genetic potentiality (Smith, 1941; see also Suomalainen, 1950, for a comprehensive review of the genetical aspects of parthenogenesis in general).

Where the maturation divisions are completely suppressed, as in *Thrinax macula* (Peacock and Sanderson, 1939), all the offspring retain precisely the same genetic constitution as the mother—so that they are daughters identical not only

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each with the other but also each with its mother. Reproduction is then essentially clonal and evolution is halted temporarily or more permanently dependent on the fortuitous occurrence of mutation or of structural rearrangement of chromosomes. It follows naturally that heterozygosity occasioned by gene mutation or other chromosome changes becomes an inescapable attribute of all descendants, for such changes cannot become homozygous. As more and more genes mutate such species assume more and more heterozygosity, for recessive genes unless immediately deleterious are not open to elimination through natural selection, but are apt to be favoured as a result of the heterosis they confer.

In species where chromosome pairing, and presumably crossing-over, are resorted to and subsequent reduction is compensated for by fusion of the second polar body with the female pronucleus, that is by auto-fertilization, segregation of genetic differences remains possible. (Failure of auto-fertilization results in males). The abandonment of heterozygosity in such a form is progressive and irrevocable, homozygosity is ultimately achieved, and the benefits associated with heterosis are thereby excluded. Maintenance of homozygosity is, in the absence of mutation and structural rearrangement of chromosomes, thus now dependent on the non-functioning of rare and genetically different males.

It therefore becomes imperative, in the final analysis of field and experimental populations, that an obligatory parthenogenetic species be determined as to category. It is already known that *D. bercyniae* belongs in the second of the above two broad types; the disposition of the larch sawfly has, until now, remained obscure. In neither case is it known whether the rare male is functional, at least in gene exchange.

As a general rule in the boreal forests of Eastern Canada, males are produced with an extremely low and irregular frequency and nothing is known as to how or why. To the south, in Minnesota, their proportion runs higher, averaging some 1.2 per cent. It is upon some 5,000 cocoons from this State, supplied by courtesy of Mr. A. T. Drooz of the U.S. Department of Agriculture, that the following observations were made. Even at the relatively high frequency of 1.2 per cent, some assortment by sex in so large a number of cocoons was obviously desirable. This was roughly achieved on the basis of size, supplemented more finely by weighing, in the expectation that males, being haploid, would be lighter than the females. About 200 small cocoons were therefore divided into four weight classes: less than 20, 20-30, 30-40, and 40-50 mg. The first group, upon dissection, proved to be dead and desiccated, as were most in the second. The two heaviest samples provided mostly living larvae, about half males and half females, although a number were parasitized. Following splitting of the cocoons, daily inspection revealed when the appropriate stages for cytological purposes were reached—white pupae, in the case of males, and prepupae, in the case of females. The methods adopted in fixation and staining were those of Smith (1943).

As expected, males proved to be haploid relative to females, that is, they have eight chromosomes in the germ line. These eight chromosomes, in spermatogonia, fall into four fairly readily recognizable types, each consisting of a similar pair: one large and one smaller V-shaped pair; one about the size of the smaller V but with a sub-median constriction; and a short V-shaped pair. The first meiotic division, as in normal males of facultative species, is abortive, all eight chromosomes going to one pole. The second division is equational and thus produces two functional sperms, each with eight chromosomes.

The diploid female has 16 chromosomes in oogonia and somatic tissue (*contra* Smith, 1941, who reported $2n=14$ for this species). In primary oocytes, the 16 chromosomes associate in pairs to form eight pachytene bivalents essentially like those of *D. bercyniae*. This pairing of the chromosomes, together with the occasional production of males, strongly implies that, by analogy with *D. bercyniae*, the first meiotic division is normal, that a second follows, and that, in all probability, diploidization of the egg is achieved by auto-fertilization. The rare failure of compensatory re-fusion would, as shown in *D. bercyniae*, then determine the production of a male. It is unfortunately not possible at present to validate this reasoning: proof must await the appropriate season of the year in order that the actual meiotic divisions, which are undergone in the newly laid eggs, may come under scrutiny. This is a tedious and time-consuming proposition that has had to be deferred due to pressure of other research commitments. It is noteworthy, however, that Comrie (1938) reported such a course of events in the European obligatory parthenogenetic *Pristiphora pallipes* Lep.

The percentage of males in English populations of *P. erichsonii* is about 2.0 according to Mangan (1910) and about 0.4 according to Hewitt (1912). That they are extremely rare in northwestern Ontario is exemplified by cocoon samples, received over a number of years by the Forest Insect Survey at Sault Ste. Marie, providing no males. A single male has, however, been found in the Kenora District of northwestern Ontario (A. M. Heimpel, pers. comm.). In New Brunswick, some 3,000 adults reared from field collections made during the last larch sawfly outbreak there provided 0.7 per cent males (Reeks, 1954). Survey records, compiled over a five-year period at Winnipeg, show percentages of 0.9 and 1.2 male emergents from Manitoba and Saskatchewan, respectively. However, adequate samples by regions from the two provinces range between zero and 2.3 per cent males, and in a fashion that indicates male production to be a matter of temperature superimposed on clonal genetic potentialities. It is important for what is to follow to note that J. A. Muldrew observed copulation on two occasions (pers. comm.), and we have already heard from Dr. Coppel that two instances are on record at Belleville.

These data are paralleled in *D. bercyniae*, where Smith (1941) postulated that the species in Canada consists of a number of biotypes distinguished by having different rates of in-sinking of the female pronucleus, that is, characteristically different potentialities for escaping diploidization. The rate was conceived as responding to differences in temperature, such as those obtaining at lower altitudes, more southerly latitudes, or under laboratory conditions, in the same way that the incubation period and the general larval development rate are known to. At higher temperatures and with particular lines, the female pronucleus was envisioned as eluding the second polar body, with consequent production of males.

Two males, from a high male-producing line carried at the Fredericton Laboratory, were induced to mate with females from the same line. The resulting sex ratios ("all to 0 and 11 to 1") differed in no significant manner from the line as a whole (R. E. Balch, pers. comm.). Unfortunately the females were not carried further, nor was fecundity or sterility recorded so that nothing is known as to whether either mating was successful. However, assuming (1) the line to be free of lethal or otherwise detrimental genes; (2) a "normal" sex ratio of $15\text{♀} : 1\text{♂}$ (see below); and (3) fertilization of 50 per cent of the eggs laid, then, from an output of 32 eggs by a mated female, 15 should be biparental, sterile triploids; 15 uniparental, parthenogenetic, diploid, and fertile females; one a

	15 x 2n	1 x 1n
Fert.	15 biparental triploids sterile	1 biparental diploid ♀ fertile
Unfert.	15 uniparental diploid ♀♀ fertile	1 uniparental haploid ♂ fertile

Fig. 1. Progeny expected following mating an obligatory parthenogenetic female by one of the rare males (for explanation see text).

biparental, diploid, and fertile female; and one a uniparental, haploid male, or a ratio of 16 ♀♀ : 1 ♂ among the viable eggs (Fig. 1).

New Brunswick material reared in the laboratory at Fredericton proved to be highly variable in its capacity to produce males, running in different lines from 396 ♀♀ : 0 ♂♂ to 150 ♀♀ : 10 ♂♂. Field observation renders highly probable the conclusion that the production of males in relatively high numbers is the joint result of a fortunate choice of an original female endowed with a low temperature-threshold being subjected to the high temperatures that prevail under laboratory conditions. If this is so, it should theoretically be possible by selection to produce females whose eggs under appropriately high temperatures would invariably remain haploid and produce only males; in other words, by selection and temperature control to induce reversion to a facultative parthenogenetic species, such as that from which it doubtless evolved. Mating such males to genetically distinct females that are subsequently compelled to oviposit at predetermined high temperatures should then ensure an avenue of exchange between different gene pools.

At temperatures that induce the production of equal numbers of reduced and unreduced eggs, mated females should engender parthenogenetic females, biparental females, haploid males, and sterile triploids in equal numbers. In fact, the proportion of sterile eggs, or of males, at any temperature, should constitute a precise measure of the efficacy of that temperature in providing an escape from the consequences of auto-fertilization. Moreover, at any temperature the two categories, males and triploids, should together equal in frequency the grouped total of parthenogenetic and biparental females, with the number of the last equalling on the average the number of males.

Muldrew (1952), through his convincing analysis of the encapsulation of the parasite *Mesoleius tenthredinis* Morley by *P. erichsonii*, has opened up the question

of the origin and genetic basis of the encapsulating ability. Is it a newly acquired attribute, originated by mutation, that, by the release it ensures, is allowing replacement, through natural dispersal, of the resident susceptible population? Or is it *Mesoleius*, itself, that is functioning as the selective mechanism in allowing the escape of those constituents of the North American *P. erichsonii* population whose expressivity for encapsulation is genotypically high? Formal genetic experimentation, incorporating the morphological differences of which we have heard from Dr. Coppel, seems no longer excluded as a method of solution of this problem.

Before concluding it might well be worth considering the taxonomic implications of obligatory parthenogenesis. The dynamic neo-Darwinian definition of the species, as opposed to the morphological species-concept of classical taxonomy, is expressed by Dobzhansky (1951, p. 262-3) in the following generally acceptable words: species are "groups of populations the gene exchange between which is limited or prevented in nature by one, or by a combination of several, reproductive isolating mechanisms". Viewed in this light, a purely parthenogenetic 'species' cannot be equated with a bisexual species, because the former comprises an indefinite number of biotypes between which gene exchange is prohibited by the absence of cross-fertilization. These divergent biotypes, having no gene pool in common, will perforce continue to diverge in the course of evolution so long as mutations continue to be incorporated in the different lines of descent. As a consequence, endeavours to establish species in such groups are doomed to failure, for as Stebbins (1950, p. 409) has said of plant taxonomists confronted with the problem, "they are looking for entities which in the biological sense are not there".

References

- Comrie, L. C. 1938. Biological and cytological observations on tenthredinid parthenogenesis. *Nature* 142: 877-878.
- Dobzhansky, Th. 1951. *Genetics and the Origin of Species*, 3rd ed. Columbia University Press.
- Hewitt, C. G. 1912. The large larch sawfly. Can. Dept. Agr. Expl. Farms Bull. No. 10—Second Series, Ent. Bull. No. 5: 1-42.
- Mangan, J. 1910. Some remarks on the parasites of the large larch sawfly *Nematus erichsonii*. *J. Econ. Biol.* 5: 92-94.
- Muldrew, J. A. 1953. The natural immunity of the larch sawfly (*Pristiphora erichsonii* (Htg.)) to the introduced parasite *Mesoleius tentbedinis* Morley, in Manitoba and Saskatchewan. *Canad. J. Zool.* 31: 313-332.
- Peacock, A. D., and A. R. Sanderson. 1939. The cytology of the thelytokous parthenogenetic sawfly *Thrinax macula*. *Trans. Roy. Soc. Edin.* 59: 647-660.
- Reeks, W. A. 1954. An outbreak of the larch sawfly (*Pristiphora erichsonii* (Htg.)) in the Maritime Provinces (Hymenoptera: Tenthredinidae) and the role of parasites in its control. *Canad. Ent.* 86: 471-480.
- Smith, S. G. 1941. A new form of spruce sawfly identified by means of its cytology and parthenogenesis. *Sci. Agr.* 21: 244-305.
- Smith, S. G. 1943. Techniques for the study of insect chromosomes. *Canad. Ent.* 75: 21-34.
- Stebbins, G. L. 1950. *Variation and Evolution in Plants*. Columbia University Press.
- Suomalainen, E. 1950. Parthenogenesis in animals. *Adv. Genet.* 3: 193-253.

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Discussion

S. A. GRAHAM (Ann Arbor): I shall make my comments very brief in order to leave time for discussion of these excellent papers by others present. Many years have passed since the larch sawfly first received attention from me, almost too many to be admitted. Beginning in 1913 and continuing into the early thirties, the closing years of the great outbreak in the Lake States was observed and a minor outbreak was followed from beginning to end in Minnesota and Michigan. During these years the information gathered led to the formulation of many ideas about the larch sawfly, many of which failed to see the light of day through publication because it was felt that more information was needed to support them.

It has now been twenty years since the sawfly has been numerous enough in Michigan to justify study. During this time the early notes have been shelved. Now that the insect is again attracting attention, I have taken my old notes from dead storage and it is very gratifying to find that the intensive work now being done, in the Canadian Laboratories, is tending to support many of my "hunches" that have been resting as unproved hypotheses awaiting favorable conditions for further study.

The fine work that has been reported today indicates an attack on the problem from numerous angles including study of the insect itself, its enemies, and the environmental conditions that influence its population growth and decline. This illustrates well that which is essential in attacking any forest insect problem. Perhaps, however, one aspect of the community approach to the study of the larch sawfly may not be receiving enough attention. Certainly it was not included for consideration in this symposium. It seems to me that more attention might well be paid to the influence of the trees that comprise the forest upon the rise and fall of insect outbreaks. The trees' age and dimension, the stand density, the trees' health, the influence of forest composition on pest numbers and other similar matters should all be included in the overall attack upon a forest insect problem.

In closing these remarks I should like to express a wish that a team of workers such as those who have delivered papers today, instead of working separately, might work together in the same laboratory where frequent personal contact would stimulate them to even finer accomplishment than has thus far been possible.

A. T. DROOZ (St. Paul): I was particularly interested in Coppel's discussion of the morphological differences between the European and American larch sawflies. It appears that current research at Belleville will resolve the confused taxonomic status of the insect. Unfortunately the status of its principal parasites is still clouded. *Mesoleius tenthredinis* is called *M. aulicus* by some, and we have a choice of either *Bessa selecta* or *B. harveyi*. I should like to show a Kodachrome slide of a larch sawfly variant. Note that the colour of the abdomen is green where it is normally orange, and orange where it is usually black.

D. M. BENJAMIN (Madison): I was particularly interested in Mr. Lejeune's comments concerning the use of life tables in the study of the larch sawfly. The life table will most certainly be of assistance in developing information about our forest insects and will enable us to better understand their bionomics.

One question I should like to raise, however, is how host information can be integrated with the life table. In species like *Neodiprion sertifer* (Geoff.), for example, the adults lay varying numbers of eggs on different pine hosts, laying a greater number of eggs on hosts of their highest preference. On pitch pine,

damage to the needles from oviposition was so severe that the needles dropped and larvae failed to hatch from them.

Work conducted by Dr. Tsao in Minnesota revealed that variations in fecundity, fertility, and larval survival of *Diprion similis* Htg. were associated with different pine host-species. This information was incorporated into a damage index which could be used to estimate the likelihood of the sawfly to be troublesome in a particular area.

C. A. MILLER (Fredericton): Have you tried frass-drop measurements as a method of assessing larval populations? This technique has been used in studies of the European spruce sawfly.

LEJEUNE: We did try collecting frass but it was difficult to relate frass drop to larval populations. With this type of insect, where the larvae drop to spin, we find direct sampling by means of larval-drop trays more efficient and reliable.

C. A. MILLER: Certain practical considerations must be taken into account in the development of life tables. The accumulation of population data may be restricted by available man-power and reliable sampling techniques require careful consideration. This is particularly true for those species inhabiting more than one 'sampling' universe as exemplified by the larch sawfly.

W. R. THOMPSON (Ottawa): It would be interesting to investigate the possibility of applying the system of life tables to the parasites themselves—this, I believe, is one of the developments that will follow as the study goes on. One of the earliest developments and I think a very clear treatment of this subject was made by Mr. W. F. Fiske in a bulletin published in 1908 on the parasites of the gypsy and brown-tail moths and in this the importance of "life tables" is very clearly recognized. I think it would be well to acknowledge the contributions made by the pioneers in this field.

G. E. SHEWELL (Ottawa): It seems incongruous that the larch sawfly larva in its cocoon should be more resistant to moisture in the dead of winter when the ground is frozen, but less resistant in spring and fall when it has every chance of being killed off by moisture.

LEJEUNE: This seems related, in part, to the supply of and demand for oxygen. When the larva first spins up, the rate of oxygen consumption is quite high, then lowered during hibernation, and raised again during the period of high mitotic activity associated with transformation into the pupa. The insects are resistant to flooding in the late fall and in the spring before mitotic activity begins. Protection afforded in the spring is particularly important, for that is the time when larch bogs are most likely to be flooded.

G. E. SHEWELL: The question of whether the palaearctic and nearctic populations of the larch sawfly represent the same or different species is very interesting to dipterists because of the related problem of the identities of their tachinid parasites of the genus *Bessa*. Workers in Washington identify this parasite, in N. America, as the European species *Bessa selecta* Mg., whereas in Ottawa, we have for some time been giving it the name *Bessa harveyi* (Tns.), a species based on N. American material. Unfortunately we have not yet found time to make a critical comparison of native material with the small amount of European material that Mr. Baird has been able to assemble for us. When, as happens from time to time, laboratory officers write to ask which of these two names is the proper one to use, we are not able to give a definite answer. It is a matter of arbitrarily choosing a name and sticking to it. On such occasions, I feel sorry for myself as a Taxonomist and envy those entomologists who have problems of a different nature.

MULDREW: A clarification of the taxonomy of *Bessa* would undoubtedly be helpful in this study. I believe many will agree that obtaining the correct identifications of both host and natural enemies before undertaking an intensive study, such as this, is of the greatest importance and perhaps should be one of the first considerations.

J. H. PEPPER (Bozeman): In studying parasites and predators, I am wondering if our attack is not just a little backwards at times. As far as I know, most of the emphasis is placed on an attempt to measure, at some particular time, the effect of parasitism and predation without attempting to determine what may have changed in the particular environment that would allow for the increased or decreased effect. The emphasis seems to be primarily on the parasite and the predator rather than on determining the conditions under which they are most effective. Again, there are times when I rather question the validity of statements made concerning effect of parasites and predators for the reason that I have never seen data which could be interpreted in terms of actual effect. Under some conditions you can find a very high degree of parasitism accompanying a distinct decrease in parasite population.

In evaluating the effect of parasites on the basis of limited measurements, I have drawn conclusions at times that I now know are erroneous. I am wondering if I may not have selected a site where a change in the environment had taken place completely unknown to me, or perhaps I had neglected to determine if such had occurred and the effect was not due to different activity on the part of the parasites, but that it was the changed environment that led the parasite to become more effective. Studies seem to be directed primarily at measuring the direct effect of parasitism and not with the idea in mind that certain segments of the environments may be changed in order to make the parasites and predators more effective.

MULDREW: In certain cases the abundance of a host insect may be drastically reduced by some such factor as starvation, frost, or an application of an insecticide, and, concurrently, the parasite population may remain relatively unaffected by this factor. Thus the percentage parasitism may show a marked and sudden rise although the actual density of the parasite remains unchanged. In such a case parasites may undeservedly be given credit for reducing an infestation. I believe that a phenomenon such as this would be revealed by using the life-table approach. I do agree with Dr. Pepper's opinion, however, that the problem of estimating the efficiency of a parasite is complicated by the fact that this efficiency is undoubtedly affected by many factors other than simple host density and much caution must be exercised in interpreting results.

J. H. PEPPER: The work of Paul Errington indicates that predation is not necessarily density dependent. Increased predation resulted from changing some security factors in the environment that caused the host to be more readily available to the predator. If such a factor is in operation, then we should be able to get just an approximation of density effect, never a true measure.

L. G. MONTEITH (Belleville): A partial answer to the question whether changes in the environment may cause a parasite to be more effective are provided by data obtained with the tachinid parasite *Drino bohémica* Mes. Changes in population levels of its preferred host, the European spruce sawfly, *Diprion hercyniae* (Htg.), definitely influence the searching behaviour of the parasite. It has a preference for unthrifty spruce trees, a condition brought on by its host and, like the host, it prefers old foliage to new growth. Changes in the foliage of

other plants following defoliation of the host's food trees also influence host searching.

It has been suggested that there is a gap between studies made with the parasites and with their hosts, that an attempt should be made to understand why parasites are associated with certain hosts. We are already studying the basic reasons for host preferences, as indicated for *D. bohémica*. Work completed or now in progress should help to bridge the gap.

C. D. F. MILLER (Ottawa): Re Buckner's paper on predation by shrews and mice, I never hear mention of predation by ants—what is the extent of predation of sawflies by ants?

MULDREW: We have not studied extensively the role of ants as a mortality factor acting against the larch sawfly but our observations indicate that they are not too important in this respect. It may be that the larch bog is a comparatively adverse habitat for ants.

A. T. DROOZ: In 1953, ants destroyed adult larch sawflies in our cold-room rearings. The ants apparently entered the cocoons as the sawflies prepared to emerge, killed the adults, and carried away parts of their bodies. We have also observed bog-inhabiting ants carrying dead sawfly larvae to their hills.

THOMPSON: In regard to ants, one of the difficulties is their very indiscriminate behaviour. In Bermuda we have been trying to control the mealy bug by means of the importation of coccinellids. Unfortunately the Argentine ant has been introduced and the only way we could get control of the mealy bug was by putting some kind of repellent band around the stem of the plants. If they are protected by ant bands the control will go on to the point where the mealy bug is practically exterminated.

A. S. WEST (Kingston): Dr. Graham may not remember that 17 years ago he visited my field laboratory in California. During our week together we had a number of stimulating discussions on approaches to the study of forest insects. Some of you may have wondered, when Dr. Graham stated that he had suggested much earlier some of the study approaches which are being used currently, if he was on solid ground. I can assure you that indeed he did foresee many of these developments.

Since 1939 Dr. Balch and I have had a number of interesting discussions on many aspects of forest entomology. It is extremely gratifying to see the progress which has been made during the past decade and more. Many, I hope, will agree with me that, although we have been concerned this afternoon with forest insects, these approaches are indeed adaptable to other groups of insects.

The ultimate goal of these studies with which we have been concerned is attempt to control forest insects. I was particularly interested in Dr. Smith's paper and its relation to Dr. Cipriani's discussion this morning. Not long ago the concept of using genetics and radiation in combination for insect control would have seemed fanciful. Today these "tools" are being used, apparently successfully, in developing a new method of control of the screw worm in the southern United States. I believe that recent results of studies being conducted on the island of Curacao will be presented in December at the meetings of the Entomological Society of America. It is not entirely beyond possibility that such "fanciful" methods may find application in other fields—perhaps even in Forest Entomology. It is evident from the discussion following today's Symposium that we have in Canada an open-minded group, and that we may expect to see still further new approaches to the study of forest insects.

Concluding Remarks

By R. E. BALCH¹

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We have had some good illustrations of different approaches to the study of forest insects. The subject has by no means been exhausted—the physiological approach, for instance, has been barely touched on—but I think the point has been brought out that there is no essential difference between the problems and methods of forest entomology and, say, agricultural entomology. There may be some differences in emphasis—the nature of the forest crop encourages the long-term ecological approach—but even this difference seems to be disappearing, as may be illustrated by Dr. Glen's recent paper on factors governing the abundance of insects.

A number of problems have been presented that arise in the study of any insect pest. In concluding the discussion I might recapitulate some of these and suggest what, to me as a forest entomologist, has been the underlying thought of the symposium.

First there is the problem of identification. To say that insects must be properly identified seems a truism. But it is not as simple as some of us in our younger days may have thought—just a matter of sending a few specimens to the appropriate taxonomist. When intensive studies of an insect are undertaken it is a not uncommon experience to find that some revision of the taxonomy is necessary. New species must be recognized, as was the case with the jack-pine budworm and the bronze poplar borer; or old ones resurrected as with the spruce sawfly; or a complex of species may be involved as in the case of the lodgepole needle miner.

The difficult task of practical systematics is to catalogue Nature and often species are man-made conveniences set up to fit very limited knowledge of the populations involved. I think the point to be emphasized here is that those of us engaged in ecological work can often uncover taxonomic problems and obtain material and biological data necessary to their solution. The taxonomist and the ecologist are interdependent.

Dr. Coppel's and Dr. Smith's papers have also brought to mind the contribution that can be made by cytological and genetic studies to the problem of identification. If reproductive isolation is the criterion of a species, such studies may provide the final word in difficult cases, especially as isolation may take many forms recognizable only by the genetic approach.

On the subject of genetics I might add in passing that studies of the inheritance of characters affecting fecundity and survival may provide the clue to otherwise baffling problems in epidemiology. The genetic constitution of populations within the species population has perhaps not received the attention it deserves as a variable in the complex of factors determining outbreaks.

One aspect of this problem of identification that has been brought out this afternoon is the recognition of introduced as opposed to native species. Sometimes the evidence of introduction is clear but I know of only one case where the time and place of introduction are known: the gypsy moth—and that is likely to remain unique. In cases such as the larch sawfly the evidence needs to be

¹Officer-in-Charge and Moderator.

critically examined. This is essential if we are to attempt generalizations about the epidemiology of introduced versus native species.

Perhaps the most difficult and fundamental problem, however, was indicated in Mr. Lejeune's paper: How to measure population trends and the factors governing them. This is essentially a question of sampling. One of the most important contributions that can be made to the study of forest insects is the development of adequate techniques for the estimation of populations at the critical stages throughout the generation. An example is the work of Morris and Miller on the spruce budworm. Population fluctuations must be measured before they can be explained. Until this problem is satisfactorily solved the factors of natural control cannot be evaluated; nor can the eventual results of introducing new factors, such as parasites, or disease, or insecticides be measured.

The measurement of populations involves, of course, the simultaneous measurement of control factors and the study of their interactions. The contributions of the Winnipeg Laboratory have illustrated the complexity of this problem. Mr. Lejeune emphasized the desirability of direct methods of estimating predator populations. Mr. Buckner showed how this was being approached in the case of small mammals, which, like birds, demand special techniques. Mr. Muldrew's discovery of the development of resistance to an introduced parasite is of particular interest. It shows the value of intensive study of the processes of parasitism. At the same time it serves to remind us of the relative impermanence of many control measures—even biological control.

One group of control factors that have been neglected until comparatively recently are the pathogenic organisms. The establishment of the Laboratory of Insect Pathology at Sault Ste. Marie has corrected this and Dr. Bird has indicated some of the progress that has been made, notably in viruses of the sawflies. Here again special techniques of sampling and rearing are necessary to determine control value. I am reminded of Dr. Bird's early work on the virus of the spruce sawfly and his solution of the problem of rearing disease-free checks with very modest equipment, which was fundamental to success in experimental studies.

The work on the spruce sawfly illustrates the importance of a close relation between specialized laboratory studies and studies of populations in the field. We must know as exactly as possible what goes on in the natural environment—in this case the occurrence and pathogenicity of the virus in the forest, and how these are affected by population density, or vice-versa. What is its place in the whole control complex? It has been shown that at the lower levels of population introduced parasites have taken the place of the disease as a major factor of control. There are some very interesting relationships between disease, parasites, predators, and host population to be worked out. This is only possible through the combination of long-term field and laboratory studies.

Which brings me to what I think has been the underlying thought of this symposium: That the various approaches to the study of forest insects are integrated by their common purpose of explaining the behaviour of natural populations. The study of population ecology is the ultimate objective of the forest entomologist and all studies eventually contribute to this end. Perhaps it might be said that the fundamental study is population ecology, and the other studies provide the foundation on which it must be based.

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Book Reviews

A MANUAL OF THE DRAGONFLIES OF NORTH AMERICA (ANISOPTERA) INCLUDING THE GREATER ANTILLES AND THE PROVINCES OF THE MEXICAN BORDER. By James G. Needham and Minter J. Westfall, Jr. University of California Press, Berkeley and Los Angeles. 1955.

This is the book that has long been awaited by all American students of Odonata and doubtless by others interested in aquatic insects in general.

Our first impression was very favourable, owing to the superb quality of the illustrations, most of which are half-tones from photographs and chiefly the work of the junior author; and to the fact that coated stock is used throughout the book, thus making it possible to have the illustrations appear as text figures, accompanying the descriptions to which they belong. Evidently a great deal of careful work has gone into the preparation of the material photographed, as well as the photographs themselves.

The illustrations include a fine frontispiece in colour, several beautiful photographs of living dragonflies, some with their cast skins; wing prints and figures of nymphs of nearly every genus and innumerable structural features.

The text is divided into two main parts of very unequal size. Part One treats of dragonflies in general, occupying 59 pages, whereas Part Two, the Systematic Classification, including glossary and index, covers the remainder of the 615 pages. Part One is divided into three sections—I. Introduction, II. Field Studies and III. Procedure.

The Introduction is admirable. Although the external features are described primarily because they are basic to classification, the many anatomical mechanisms peculiar to dragonflies, such as that of the nymphal labium, are so vividly presented that the subject never grows tedious in the way that anatomical descriptions are wont to do.

In the Field Studies, which deal with the habits and life histories of dragonflies in general, methods of collecting and rearing and the preparation of material, several novelties are described, such as the use of swatters for capturing dragonflies that sit flat on the ground, and the dark cage for keeping dragonflies alive and in good condition to await an opportunity for photographing them.

Under III, Procedure, the student obtains guidance in the use of the Manual, as in the explanation of abbreviations and other devices for saving space. It also contains a complete list of the genera and species treated in the Manual, with the pronunciation of the names indicated.

Part Two is almost exclusively taxonomic. In addition to the descriptions and keys to families, genera and species, in both nymphal and adult stages, it contains many tables that summarize many of the characters, in order to facilitate a general survey of the members of a group, such as the species of a genus. In dealing with the large number of species covered in the Manual, everything possible must be done to save space. Hence, when a part is figured, description is usually reduced to a minimum; and when colour pattern suffices for the recognition of a species, the figure is generally omitted. In the larger and more difficult genera figures of the anal appendages, and in Gomphidae also the hamules, are included. Distribution is indicated by states and provinces, those of each group arranged in alphabetical order.

The number of genera treated in the Manual is 70 (including 5 subgenera of *Gomphus* listed with the genera); the number of species and "varieties" is 332. Four genera and 33 species are not recorded north of Mexico. The distribution

of species in families is as follows (genera in brackets): Petaluridae (2)2; Cordulegasteridae (1)8; Gomphidae (14)95; Aeshnidae (11)45; Libellulidae (44)182. The Libellulidae include the subfamilies Macrominae (2)13; Cordulinae (8)50; and the Libellulinae (33)119.

In a work that covers such a vast quantity of material as the Manual, errors and omissions are inevitable. There are very few typographical errors but of other inaccuracies and omissions we have found a fair number, although they are not serious enough to be listed. The transposing of figures 188 and 189 should be noted, if only because they are so much alike. Otherwise we shall refer only to what appears to us a tendency to give too much attention to venation in the description of *species* and not enough to other features of colour and form, which are often more specific. So little attention is given to female characters that no mention is made of the colour dimorphism of females, in which the colour may be the same as in the male (homoeochromatic) or it may be more or less strikingly different (heterochromatic). In *Aeshna constricta*, for example, the female may be blue-spotted like the male or it may be of various shades of green to a vivid yellow green. All that is said of the female in the Manual is "Female similar to male but paler". Another somewhat different case is that of *Sympetrum obtrusum*, in which the abdomen of the mature male is red, that of the female dull yellow (only very rarely red). The female of the nearly related *S. internum* is red in both sexes. Yet in the Manual *obtrusum* is said to be "Very similar to *internum*, to be distinguished only by critical examination of the genitalia of abdominal segment 2." If this statement is intended to apply to males only, it may be noted that not only are the two species different in the form of the abdomen but the face of *obtrusum* is creamy white, while that of *internum* is cherry red. (This difference is noted in the key to species.)

In spite of these minor criticisms we return to our original impression that the Manual is a fine achievement. It should certainly have a place in every entomological and limnological library and will undoubtedly remain the most important general source of information on North American Anisoptera for many years to come.

E. M. WALKER

MOSQUITOES, THEIR BIONOMICS AND RELATION TO DISEASE, by William R. Horsfall; 723 pp., 206 Tables. The Ronald Press Company, New York. 1955. Price \$16.00.

This book is a mine of information on the bionomics of mosquitoes. It is a work of reference that all students of these insects will find useful and it should have a place in all entomological libraries. During its compilation the author scanned over 12,000 papers, and of these about 4,000 are recorded in the bibliography of 76 pages. The text is very largely (pp. 41-600) devoted to a consideration of the species one by one; the author's system is to classify the information about the four stages under a series of headings and to give a brief abstract of the findings reported in the relevant papers. Comment by the author himself is in most cases slight.

Unfortunately, the metaphor of a mine is apt, and the information has to be quarried, dressed and built up by the reader. There is no synthesis. The book is in no sense a more complete and fully documented 'Marston Bates', and even in the treatment of a particular species the synthesis of successive reports is often

meagre. Information is tabulated under the name of the species on which the study was made, whether it is a question of the details of the habitat of the larva or of a matter of broad import such as the study of Wigglesworth on the tissue storage of reserve nutrients. The introductory section of the book, containing general material, is short (pp. 7-40), somewhat fragmentary and not entirely satisfactory; there is no subject index; and the bibliography quotes references only, without titles. Except by reading the whole book, there is, therefore, no means of finding a particular subject, even if the subject has been discussed; or of obtaining information on a simple comparative point such as, for instance, which mosquitoes lay their eggs in rafts.

A great number of species are treated, either in separate articles or, with little-known species, in tables of summary. The Index of Genera and Species lists not only those mentioned in the text, but also those whose habits, presumably, are unknown; it thus becomes a catalogue of the mosquitoes of the world up to 1952 or 1953. The problem of nomenclature, however, is not completely solved. The author states his position thus: "The criterion used to determine which [name] to apply was that common among systematists of the group". This principle of course leads to legitimate differences of opinion; thus the well known frog-biting *Culex* is still *C. territans* Walker, although it is now generally referred to as *C. apicalis* Adams, while the classical *Megarhinus* has metamorphosed into *Toxorhynchites* so completely that the former is not even mentioned in the index.

In spite of these shortcomings, the book has an obvious value. If information on a particular species is required, the relevant article gives an abstract of all, or almost all, that has accumulated, with references. The literature on mosquitoes being as voluminous as it is, it is perhaps difficult to ask for much more, even from a work of seven hundred pages.

J. A. DOWNES

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